PROCEEDINGS

OF THE

ROYAL SOCIETY OF VICTORIA

Volume 103

1991

CONTENTS OF VOLUME 103

ERRATUM

The contents page for Volume 102 of the *Proceedings*, issued with Number 2 of that volume, contained a typographical error in the heading. Please replace that page with the amended contents list attached.

THE ANT FAUNA OF A MALLEE OUTLIER NEAR MELTON, VICTORIA

Alan N. Andersen[1,3], Bronwyn A. Myers[1]
and Karen M. Buckingham[2]

[1]School of Botany, University of Melbourne, Parkville, Victoria 3052
[2]Department of Zoology, University of Melbourne, Parkville, Victoria 3052
[3]Present address: Division of Wildlife and Ecology, CSIRO Tropical Ecosystems Research Centre, PMB 44 Winnellic, Northern Territory 0821

Andersen, A. N., Myers, B. A. & Buckingham, K. M., 1991:06:30. The ant fauna of a mallee outlier near Melton, Victoria. *Proceedings of the Royal Society of Victoria* 103 (1): 1–6. ISSN 0035-9211.

Long Forest mallee, near Melton, Victoria, occurs 110 km from the nearest other mallee vegetation and is therefore of considerable biogeographic interest. Ants were sampled directly by hand and by pitfall trapping during 1983–1985, with a total of 77 species from 21 genera recorded. The fauna was dominated by the meat ant, *Iridomyrmex purpureus* (29% of all ants in traps), with species of *Monomorium* (8 species, total of 25% of all ants), *Pheidole* (5 species, 13% of all ants), and *Notoncus "enormis"* (8% of all ants) also abundant. In many respects the fauna resembles that at Wyperfeld National Park located in the major mallee region of northwestern Victoria: many species and species-groups are shared, and the overall biogeographical profiles and composition of functional groups are similar. However, the Long Forest fauna has several important differences which reflect the site's southerly location, including a lower species to genus ratio, a lower representation of Eyrean taxa, a higher abundance of Bassian elements, and the occurrence of some species characteristic of cooler and wetter parts of southern Victoria.

AN ISOLATED outlier of mallee vegetation (hereafter referred to as Long Forest mallee) occurs south of the Great Dividing Range in a rain-shadow area (mean annual rainfall approximately 500 mm) near Melton, 50 km west of Melbourne. It is by far the most southerly patch of mallee in southeastern Australia, occurring 110 km southeast from the nearest similar vegetation at Bendigo. Several plant species found in Long Forest mallee, such as *Rhagodia parabolica* (only found in Victoria in the immediate region), *Sclerolaena diacantha* and *Myoporum deserti*, are characteristic of the arid zone (Myers et al. 1986).

The insect fauna of Long Forest mallee is poorly known but clearly is of considerable biogeographic interest. Here we document the ant fauna of a site within Long Forest mallee and compare it with those of two well-studied sites which represent biogeographic contrasts in Victoria. One of these sites is at Wyperfeld National Park (mean annual rainfall approximately 400 mm) in the major mallee region of semi-arid northwestern Victoria (Andersen 1983, 1984, Andersen & Yen 1985), and the other is Wilsons Promontory (mean annual rainfall 1000–1200 mm) on the southern coast (Andersen 1986a, b, 1988). These sites support contrasting ant faunas. The major elements at Wilsons Promontory are Bassian taxa (Andersen 1991a) such as the *nitidiceps–foetans* complex of *Iridomyrmex*, *Rhytidoponera tasmaniensis*, *R. victoriae*, and species of *Notoncus* and *Prolasius*. Arid-adapted (Eyrean) taxa such as *Melophorus* spp. are poorly represented. A substantial number of Bassian elements are also present at Wyperfeld but they occur within a framework of predominantly arid-adapted taxa, particularly species of *Iridomyrmex*, *Camponotus* and *Melophorus*. These three genera represent the "core" taxa of Australian arid-zone communities, together usually contributing about half the total species (Greenslade 1979, Greenslade & Greenslade 1989).

STUDY SITE

Long Forest mallee is described in detail by Myers et al. (1986). It occupies an area of approximately 1.5 km² (it was three times this size before clearing commenced 25 years ago), and is dominated by the mallee eucalypt *E. behriana* of up to 10 m in height, with a sparse understorey of grasses, perennial herbs and chenopods. The soil is a Tertiary sandy clay. The study was conducted within an area of approximately 1 ha, located in a property owned by Dr and Mrs M. Baker.

METHODS

Ants were sampled between 1983 and 1985 by collecting them directly from the ground and from vegetation, and by pitfall trapping. Pitfall traps were 35 mm diameter plastic vials, partly filled with 70% ethanol, which were buried with their rims flush to the soil surface. Traps were similar to those used at Wilsons Promontory and Wyperfeld, and the catches are likely to provide a good indication of the relative abundance of species on the ground (Andersen 1983, 1986a, 1991b). The traps were arranged in a 5 × 6 grid with 5 m spacing (area of grid 500 m²), and operated for 4-day periods during January 1983, October 1983 and May 1985. Hand collections were conducted during these periods and also on other occasions covering all seasons. Ant species captured in traps were scored according to a five point abundance scale (1 = 1 ant; 2 = 2–5 ants; 3 = 6–20 ants; 4 = 21–50 ants; 5 = > 50 ants) in order to reduce distortions caused by large numbers of ants falling into a few traps (see Andersen 1991b). These abundance scores were used directly as counts when calculating relative abundances.

Most of the ants collected could not be identified to species with certainty because of our generally poor taxonomic knowledge of Australian ants. Where possible, these species were assigned to informal species-groups (denoted by inverted commas, eg. *Camponotus "claripes"*) derived by the senior author from type specimens held in the Museum of Victoria and in the Australian National Insect Collection, CSIRO Division of Entomology, Canberra (see Andersen 1991a). A complete set of voucher specimens is held by the senior author.

In the absence of a published biogeographic treatment of the Australian ant fauna, each species was judged to belong to groups with Bassian, Eyrean or widespread distributions according to the senior author's understanding of Australian ants. The pattern of community organisation was investigated by classifying species into functional groups according to their presumed habitat requirements and competitive interactions. This classification is modified from Greenslade (1978), and has been used extensively in studies of Australian ant communities (see Greenslade & Greenslade 1989, Andersen 1990, 1991c).

The biogeographic profile and pattern of community organisation of the Long Forest mallee fauna was compared with those of Wyperfeld and Wilsons Promontory. The species lists from these other localities were obtained from detailed studies of small plots, as at Long Forest mallee. The Wilsons Promontory data are from two woodland sites each of approximately 0.25 ha (Andersen 1986a, 1988), and the Wyperfeld data are from adjacent heath and mallee sites each of 0.13 ha (Andersen 1983, 1984, Andersen & Yen 1985).

RESULTS

A total of 77 species from 21 genera were collected (see appendix), with 44 of these caught in traps. The species accumulation curve (Fig. 1) suggests that the number of species occurring in the 500 m² trapping grid was in excess of 50. The richest genera were *Camponotus* (12 species), *Monomorium* (11), *Iridomyrmex* (8), *Myrmecia* (7), *Melophorus* (5) and *Pheidole* (5). The mean number of species per genus was 3.7, midway between that at Wilsons Promontory (2.9) and at Wyperfeld (4.6). *Iridomyrmex, Camponotus* and *Melophorus* together contributed 32% of total species at Long Forest mallee, again midway between Wilsons Promontory (23%) and Wyperfeld (42%).

The biogeographic profile of the Long Forest mallee fauna resembles that at Wyperfeld far
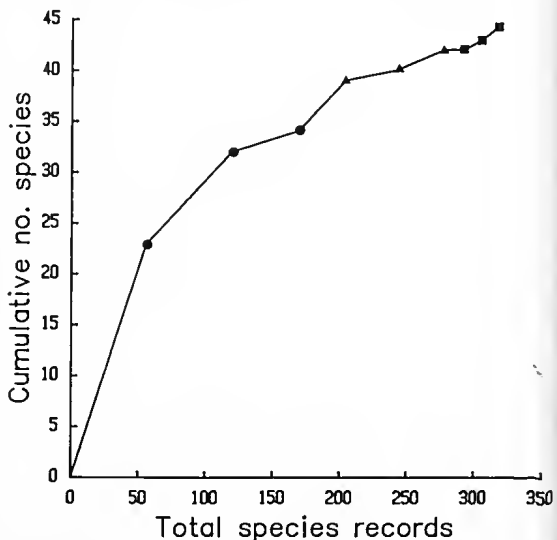

Fig. 1. Accumulation of ant species in pitfall traps (500 m² grid) at Long Forest mallee. Each point represents the running total of ten traps (circles = January 1983; triangles = October 1983; squares = May 1985). Number of species records is the sum of the total number of species recorded in each trap, regardless of species turnover across traps.

	Bassian	Eyrean	Widespread
Long Forest mallee (n = 77)	16	21	64
Wilsons Promontory (n = 83)	37	5	58
Wyperfeld (n = 138)	17	28	55

Table 1. Biogeographical profile of the Long Forest mallee ant fauna (see appendix for biogeographic affinities of individual species) compared with those at Wilsons Promontory (combined lists of Andersen 1986a, 1988) and Wyperfeld (list of Andersen & Yen 1985). Data are the percentages of species having Bassian, Eyrean and widespread distributions.

more than Wilsons Promontory (Table 1). The proportions of Bassian taxa are very similar at the first two locations (16% and 17% respectively, compared with 37% at Wilsons Promontory), with Eyrean taxa being slightly less prominent at Long Forest mallee (21% *versus* 28%, compared with 5% at Wilsons Promontory). The closer affinities of the Long Forest mallee fauna to that at Wyperfeld is further suggested by the distributions of individual species and species-groups. Of the 35 Long Forest taxa identified at this level, 15 (*Myrmecia* sp. nr *inandibularis, M. ?dichospila, M. "nigriceps", M. "tepperi", Mesostruma loweryi, Monomorium "insolescens", Podomyrma adelaidae, Iridomyrmex "discors", I. "nitidus", I. purpureus, Camponotus "ephippium", C. "suffusus", C. "tricoloratus", Notoncus "enormis"* and *Polyrhachis phryne*) occur at Wyperfeld but not Wilsons Promontory, whereas the reverse is true for only five (*Myrmecia ureus, Rhytidoponera tasmaniensis, Monomorium "flavigaster", Tapinoma "minutum"* and *Notoncus "ectatommoides"*). The occurrence of *Myrmecia forceps* at Long Forest mallee appears to be the first record of this species in Victoria (see Clark 1951, Taylor & Brown 1985).

Dominant species of *Iridomyrmex* comprised 31% of all ants captured in pitfall traps at Long Forest mallee (Table 2). *Iridomyrmex purpureus*, a member of the meat ant complex (Greenslade 1976, Greenslade & Halliday 1982), was by far the leading dominant, comprising 29% of total catches (93% of total *Iridomyrmex*). The other major functional group was "generalised Myrmicinae" (mostly species of *Monomorium* and, to a lesser extent, *Pheidole*), which comprised 39% of total catches. "Associated subordinate Camponotinae" (primarily species of *Camponotus*) and "hot and cold climate specialists" contributed many species, but, aside from

Notoncus "enormis" (8% total catches), none were frequently recorded in traps.

Functional group composition at Long Forest mallee is extremely similar to that at Wyperfeld, the correlation (r; n = 9) between percentage abundance sub-totals in Table 2 being 0.97. The only substantial difference is the relatively high abundance of "cold climate specialists" (primarily *N. "enormis"*) at Long Forest mallee (Table 2). However, although the total relative abundance of "generalised Myrmicinae" was similar, species of *Pheidole* and *Monomorium* were respectively more and less prominent at Long Forest mallee. The sub-totals in Table 2 for Wilsons Promontory are not related (r = –0.17, p > 0.05) to those for Long Forest mallee.

DISCUSSION

The ant fauna of Long Forest mallee is very similar to that at Wyperfeld in terms of its biogeographical profile (Table 1) and functional group composition (Table 2). Many species and species-groups occur at both sites. However, there are several important differences, all of which reflect the Long Forest mallee's higher rainfall and southerly location. The differences are: a lower species to genus ratio; a lower representation of Eyrean taxa (Table 1), particularly *Melophorus* (Table 2); a higher abundance of Bassian elements (*Notoncus*, Table 2); and the occurrence of some species characteristic of cooler and wetter parts of southern Victoria (such as *Rhytidoponera tasmaniensis*). The Long Forest site can therefore be described as supporting an ant fauna essentially typical of the mallee region of northwestern Victoria, but with a somewhat greater Bassian influence.

Several Bassian taxa that occur at Wyperfeld were not recorded at Long Forest mallee. These include *Iridomyrmex "itinerans"* and species of *Dolichoderus* and *Prolasius*. It is possible, however, that these taxa are present locally but outside the study site. A larger number of Eyrean and arid-adapted tropical taxa that occur at Wyperfeld were also not recorded at Long Forest mallee, and many of these probably do not occur there. They include species of *Cerapachys, Monomorium ("Chelaner")* (eg. *"rothsteini", "whitei"), Tetramorium, Camponotus* (eg. *"aurocincta", whitei), Melophorus* (eg. *"aeneovirens"*) and *Opisthopsis*.

The Long Forest site is a mallee ecosystem on Melbourne's doorstep. It has suffered from poor management decisions in the past but is now a

	Long Forest	Wyperfeld	W Prom
1 Dominant Dolichoderinae			
Iridomyrmex	5 (31)	13 (35)	8 (18)
sub-total	5 (31)	15 (35)	8 (18)
2 Associated Subordinate Camponotini			
Camponotus	12 (4)	29 (2)	3 (9)
Polyrhachis	1 (—)	5 (—)	2 (—)
sub-total	13 (4)	34 (2)	5 (9)
3a Hot Climate Specialists			
Meranoplus	10 (2)	3 (1)	0
Monomorium ("Chelaner")	2 (—)	4 (—)	0
Podomyrma	1 (—)	1 (—)	0
Melophorus	5 (—)	13 (8)	0
sub-total	18 (3)	22 (9)	0
3b Cold Climate Specialists			
Epopostruma	1 (—)	2 (—)	0
Mesostruma	1 (—)	1 (—)	0
Monomorium ("Chelaner")	1 (—)	0	4 (4)
Podomyrma	1 (—)	2 (—)	1 (—)
Myrmecorhynchus	1 (—)	0	0
Notoncus	3 (8)	3 (—)	1 (10)
sub-total	8 (8)	15 (—)	9 (14)
4a Cryptic Species			
Hypoponera	1 (—)	0	1 (—)
Solenopsis	2 (1)	1 (—)	1 (14)
sub-total	3 (1)	4 (—)	3 (14)
4b Sub-cryptic Species			
Iridomyrmex "darwinianus"	2 (3)	1 (9)	0
I. "glaber"	1 (1)	2 (—)	0
Tapinoma	1 (—)	0	1 (—)
Paratrechina "minutula"	1 (7)	1 (—)	1 (—)
Stigmacros	2 (2)	13 (2)	3 (—)
sub-total	7 (13)	17 (11)	6 (5)
5 Opportunists			
Rhytidoponera	1 (1)	0	2 (27)
sub-total	1 (1)	5 (—)	3 (37)
6 Generalised Myrmicinae			
Crematogaster	1 (1)	6 (3)	1 (—)
Monomorium	8 (25)	8 (35)	1 (—)
Pheidole	5 (13)	6 (4)	4 (1)
sub-total	14 (39)	22 (42)	6 (1)
7 Large, Solitary Foragers			
Myrmecia	7 (—)	4 (—)	5 (2)
Trachymesopus	1 (—)	0	0
sub-total	8 (—)	4 (—)	6 (2)
Total	77 (100)	138 (100)	47 (100)

Table 2. Ant community organisation at Long Forest mallee compared with that at Wyperfeld (combined heath and mallee plots, data from Andersen 1983, Andersen & Yen 1985) and Wilsons Promontory (data from woodland site in Andersen 1986a). Taxa are classified into functional groups according to their habitat requirements and competitive interactions (see text). Data are numbers of species per taxon and, in brackets, their percentage abundance in pitfall traps (dashes indicate less than 1%).

Victorian National Parks and Wildlife Service Reserve. Its unique biogeography make it a significant part of Victoria's natural heritage.

ACKNOWLEDGEMENTS

REFERENCES

ANDERSEN, A. N., 1983. Species diversity and temporal distribution of ants in the semi-arid mallee region of northwestern Victoria. *Australian Journal of Ecology* 8: 127–137.

ANDERSEN, A. N., 1984. Community organization of ants in the Victorian mallee. *Victorian Naturalist* 101: 248–251.

ANDERSEN, A. N., 1986a. Diversity, seasonality and community organization of ants at adjacent heath and woodland sites in southeastern Australia. *Australian Journal of Zoology* 34: 53–64.

ANDERSEN, A. N., 1986b. Patterns of ant community organization in mesic southeastern Australia. *Australian Journal of Ecology* 11: 87–99.

ANDERSEN, A. N., 1988. Immediate and longer term effects of fire on seed predation by ants in southeastern Australia. *Australian Journal of Ecology* 13: 285–293.

ANDERSEN, A. N., 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proceedings of the Ecological Society of Australia* 16: 347–357.

ANDERSEN, A. N., 1991a. *The Ants of Southern Australia: A Guide to the Bassian Fauna.* CSIRO Press, Melbourne.

ANDERSEN, A. N., 1991b. Sampling communities of ground-foraging ants: pitfall catches compared with quadrat counts in an Australian tropical savanna. *Australian Journal of Ecology* 16 (in press).

ANDERSEN, A. N., 1991c. Parallels between ants and plants: implications for community ecology. In *Ant-Plant Interactions*, C. R. Huxley & D. F. Cutler, eds, Oxford University Press, 539–558.

ANDERSEN, A. N. & YEN, A. L., 1985. Immediate effects of fire on ants in the semi-arid mallee region of northwestern Victoria. *Australian Journal of Ecology* 10: 25–30.

CLARK, J., 1951. *The Formicidae of Australia I. Subfamily Myrmeciinae.* CSIRO Press, Melbourne.

GREENSLADE, P. J. M., 1976. The meat ant *Iridomyrmex purpureus* (Hymenoptera: Formicidae) as a dominant member of ant communities. *Journal of the Australian Entomological Society* 15: 237–240.

GREENSLADE, P. J. M., 1978. Ants. In *The Physical and Biological Features of Kunoth Paddock in Central Australia*, W. A. Low, ed., CSIRO Division of Land Resources Management Technical Paper No. 4.

GREENSLADE, P. J. M., 1979. *A Guide to Ants of South Australia.* South Australian Museum, Adelaide.

GREENSLADE, P. J. M. & GREENSLADE, P., 1989. Ground layer invertebrate fauna. In *Mediterranean Landscapes in Australia: Mallee Ecosystems and Their Management*, J. C. Noble & R. A. Bradstock, eds, CSIRO Press, Melbourne, 266–284.

GREENSLADE, P. J. M. & HALLIDAY, R. B., 1982. Distribution and speciation in meat ants, *Iridomyrmex purpureus* and related species (Hymenoptera: Formicidae). In *Evolution of the Flora and Fauna of Arid Australia*, W. R. Barker & P. J. M. Greenslade, eds, Peacock, Adelaide, 249–255.

MYERS, B. A., ASHTON, D. H. & OSBORNE, J. A., 1986. The ecology of the mallee outlier of *Eucalyptus behriana* F. Muell. near Melton, Victoria. *Australian Journal of Botany* 34: 15–39.

TAYLOR, R. W. & BROWN, D. R., 1985. Hymenoptera: Formicoidea. In *Zoological Catalogue of Australia*, vol. 2, *Hymenoptera: Formicoidea, Vespoidea and Sphecoidea*, Australian Government Publishing Service, Canberra, 5–159.

APPENDIX

List of ant species recorded at Long Forest mallee. Authorities for species names are given in Taylor & Brown (1985). The biogeographical affinity of each species (B = Bassian, E = Eyrean, W = widespread) is also given.

MYRMECIINAE

Myrmecia (teperri gp) *dixoni* (W)
M. (nigriceps gp) *fasciata* (W)
M. forceps (W)
M. (urens gp) *?dichospila* (W)
M. pyriformis (W)
M. urens (W)
M. (mandibularis gp) sp. (W)

PONERINAE

Hypoponera sp. (W)
Rhytidoponera tasmaniensis (B)
Trachymesopus rufoniger (B)

MYRMICINAE

Crematogaster sp. (W)
Epopostruma "quadrispinosa" (B)

Meranoplus spp. (× 10; W)
Mesostruma loweryi (B)
Monomorium (*"Chelaner"*) *"insolescens"* (2 spp.; E)
M. (*"Chelaner"*) *"flavigaster"* (B)
Monomorium spp. (× 8; W)
Pheidole spp. (× 5; W)
Podomyrma adelaidae (B)
P. ?rugosa (B)
Solenopsis spp. (× 2; W)

DOLICHODERINAE

Iridomyrmex *"bicknelli"* (E)
I. *"darwinianus"* (2 spp.; W)
I. *"discors"* (E)
I. *"glaber"* (W)
I. *"gracilis"* (E)
I. *"nitidus"* (W)
I. purpureus (E)
Tapinoma *"minutum"* (W)

FORMICINAE

Camponotus (*suffusus* gp) *bendigensis* (E)
C. *"claripes"* (3 spp.; W)
C. (*consobrinus–nigriceps* gp) *obniger* (W)
C. *"ephippium"* (2 spp.; E)
C. *"nigroaeneus"* (2 spp.; W)
C. *"rubiginosus"* (W)
C. *"tricoloratus"* (E)
C. suffusus (E)
Melophorus *"hirsutus"* (E)
Melophorus spp. (× 4; E)
Myrmecorhynchus *"emeryi"* (B)
Notoncus *"ectatommoides"* (B)
N. *"enormis"* (B)
N. *"hickmani"* (B)
Paratrechina *"minutula"* (W)
Polyrhachis phryne (B)
Stigmacros (*"Campostigmacros"*) sp. (W)
S. (*"Stigmacros"*) sp. (W)

THE BEALIBA METEORITE FROM VICTORIA

William D. Birch

Department of Mineralogy and Petrology, Museum of Victoria,
285 Russell Street, Melbourne, Victoria 3000

BIRCH, W. D., 1991:06:30. The Bealiba Meteorite from Victoria. *Proceedings of the Royal Society of Victoria* 103 (1): 7–11. ISSN 0035-9211.

The Bealiba Meteorite is an L6 chondrite discovered in the collections of the Geological Survey of Victoria. The single 652 gram specimen was donated to the Geological Survey in 1950 by J. E. Renshaw but was not recognised as a meteorite. The collecting site was given as "one mile north of Bealiba", Victoria. The meteorite consists of poorly defined chondrules and irregular metallic grains in a recrystallised matrix. The main minerals present are orthopyroxene, olivine, oligoclase, troilite, kamacite, taenite, diopside and chromite. Microprobe analyses of these minerals are typical of L6 chondrites. Goethite alteration occurs around the Fe–Ni grains and in veinlets in the groundmass. The Bealiba Meteorite is the second L6 chondrite discovered in Victoria.

THE BEALIBA meteorite is a previously unrecorded L6 chondrite, with a fall site near the small central Victorian town of Bealiba (36°48′ S, 143°33′ E), about 30 km northwest of Maryborough (Fig. 1). The specimen was discovered during early 1989 in the collections of the Geological Survey of Victoria (GSV), following their transfer to the Museum of Victoria in 1987. The author recognised the meteorite while sorting a tray of miscellaneous rocks. It was registered in the GSV collection as no. 11635 and labelled as "ironstone with sandstone", from 1 mile north of Bealiba, Victoria. It had been donated to the GSV by Mr J. Renshaw in October 1950. The Bealiba meteorite is now registered as no. E12275 in the collection of the Department of

Fig. 1. Locality map showing the likely discovery and fall site of the Bealiba Meteorite, the former Renshaw paddock (stippled block), 1.6 km northwest of Bealiba, Victoria.

Mineralogy and Petrology, Museum of Victoria. The name, together with data for classification, were approved by the Nomenclature Committee of the Meteoritical Society early in 1990.

HISTORY OF DISCOVERY

In order to verify the original fall site, attempts were made to contact surviving members of the Renshaw family. Two sisters, Alva and Mary Renshaw, of Newstead, Victoria, confirmed that their late brother, Joseph E. Renshaw (1907–1977), was an avid collector of geological specimens and spent considerable time fossicking in bushland around Bealiba. He also paid regular visits to the GSV Museum in Melbourne. The father of the family, Joseph A. Renshaw, ran a drapery in Bealiba and owned a 10-acre "paddock" north of the town. This block is presumed to be the original fall and discovery site (Fig. 1).

A visit to the block (Fig. 2), about 1.6 km northwest of Bealiba, showed it to be situated on the southern slopes of a small hill. The country is now lightly wooded but was probably largely clear of trees in 1950. The block has recently been sold as part of a rural residential development.

GEOLOGY OF THE SITE

Weathered yellowish Lower Ordovician marine siltstones and shales, with a north–south strike, outcrop on the block. Some fragments of white reef quartz are also present. In such an area, a meteorite would look out of place to a keen geological observer.
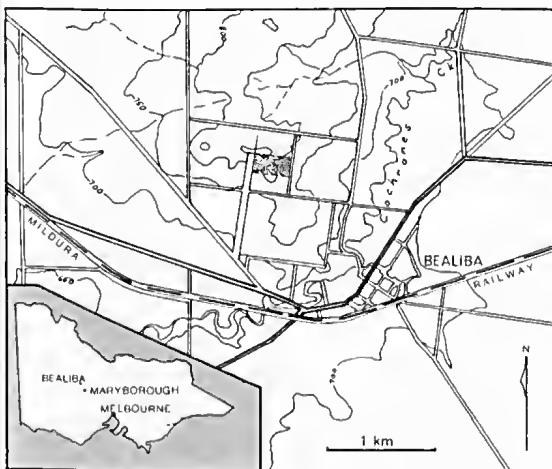
Fig. 2. The present-day appearance of the Renshaw paddock, in foreground, looking southeast towards Mt Bealiba.

FEATURES OF THE METEORITE

The meteorite is roughly equidimensional and measures 90 by 80 by 55 mm. Its thin, dark brown fusion crust is nearly complete, apart from where a small portion had been broken off one end, possibly on impact (Fig. 3A). The exposed area, roughly 75 by 50 mm, has the texture of weathered buff-coloured sandstone, with scattered patches of dark brown iron oxide staining several millimetres across. The specimen had a mass of 652 g and a density of 3.9 g/cc prior to removal of a slice for thin sectioning. A glassy tumulose patch, 20 mm across, occurs on one surface (Fig. 3B). This feature is not associated with any internal textural variation and may have been caused by the application of a high
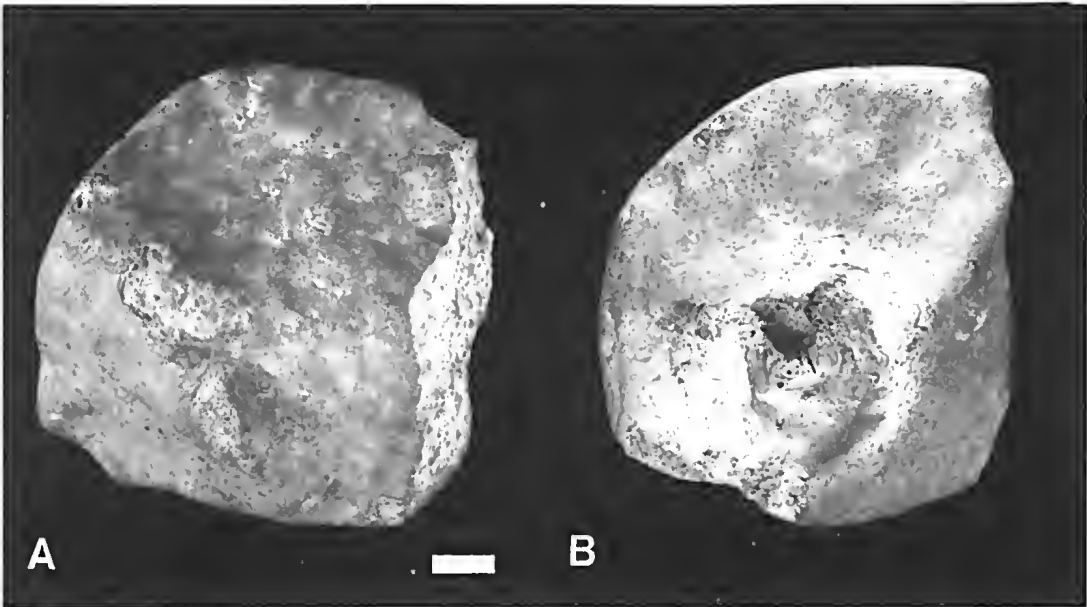

Fig. 3. The Bealiba Meteorite showing (A) fusion crust with missing portion removed on impact, and (B) tumulose patch caused by artificial heat source. Scale bar is 10 mm.

temperature heat source, such as an oxy-acety-lene flame, by the finder.

PETROGRAPHY AND MINERALOGY

In thin section, the Bealiba meteorite shows plentiful but mostly poorly defined chondrules up to 2.5 mm across, together with irregular met-allic grains up to 2.5 mm across, in an exten-sively recrystallised granular matrix which has been heavily stained with iron oxides. The main groundmass minerals are olivine, with less abun-dant orthopyroxene and interstitial oligoclase. Glass is absent. The chondrules may be fine-grained or barred olivine or orthopyroxene types, with minor clinopyroxene and interstitial sodian feldspar. Others consist of a distinct annulus of olivine and a core of rounded olivine grains in optical continuity (Fig. 4).

Microprobe analysis (Table 1) showed the olivine in both the groundmass and chondrules to be quite uniform in composition. Six analyses gave an average formula of $Fo_{74.6}Fa_{24.9}Te_{0.5}$ (mol%). The orthopyroxene is Mg-rich ("bron-zite") with an average composition expressed by $En_{77}Fs_{21.5}Wo_{1.5}$ (average of 5 analyses), and the uncommon clinopyroxene is diopside (Fig. 5). The interstitial oligoclase is $Ab_{83}An_{11}Or_6$.

The main metallic minerals in the meteorite are kamacite, troilite and taenite, which together

Fig. 4. Olivine chondrule 1 mm in diameter, showing distinct annular rim and etched core in optical con-tinuity.

constitute about 5% of the stone. Kamacite oc-curs as irregular grains up to 2 mm across, showing as creamish white and highly reflective in incident light. Taenite is not as common and generally forms smaller grains, although some of the larger grains show the two minerals in sharp contact. The taenite may be distinguished by its slightly greyer colour, but unless the two min-erals are in contact they cannot easily be dis-tinguished optically. Troilite is as common as kamacite and forms irregular pale brownish

	1	2	3	4	5
SiO_2	37.76	64.78	55.40	54.07	—
TiO_2	0.02	—	0.26	0.55	3.31
Al_2O_3	—	19.78	0.15	0.46	6.21
Fe_2O_3	—	1.83	0.56	—	—
Cr_2O_3	—	—	0.13	0.64	54.50
NiO	—	—	0.06	0.08	—
FeO	23.10	—	14.54	5.25	31.65
MnO	0.41	—	0.38	0.23	—
MgO	38.21	0.87	28.14	16.19	2.27
CaO	—	2.16	1.01	22.07	—
Na_2O	—	9.70	—	0.60	—
K_2O	—	1.12	—	—	—
Total	99.50	100.24	100.53	100.14	97.94

1. Olivine (chondrule rim) $Fo_{74.4}Fa_{25.2}Te_{0.4}$
2. Oligoclase (groundmass) $Ab_{83.4}An_{10.3}Or_{6.3}$
3. Orthopyroxene (g'mass) $En_{75.5}Fs_{22.5}Wo_{2.0}$
4. Diopside (in chondrule) $En_{46.1}Wo_{45.2}Fs_{8.7}$
5. Chromite (groundmass)

Table 1. Microprobe analyses of non-metallic minerals in the Bealiba Meteorite. Analyses obtained using Camaca and Jeol microprobes at 15 kV and specimen current 0.02 µA. Standards included corundum (Al), wollastonite (Ca, Si), pure metals (Cr, Ni, Mn), hematite (Fe), jadeite (Na), rutile (Ti) and synthetic KTa (K). Fe partitioned by stoichiometry.
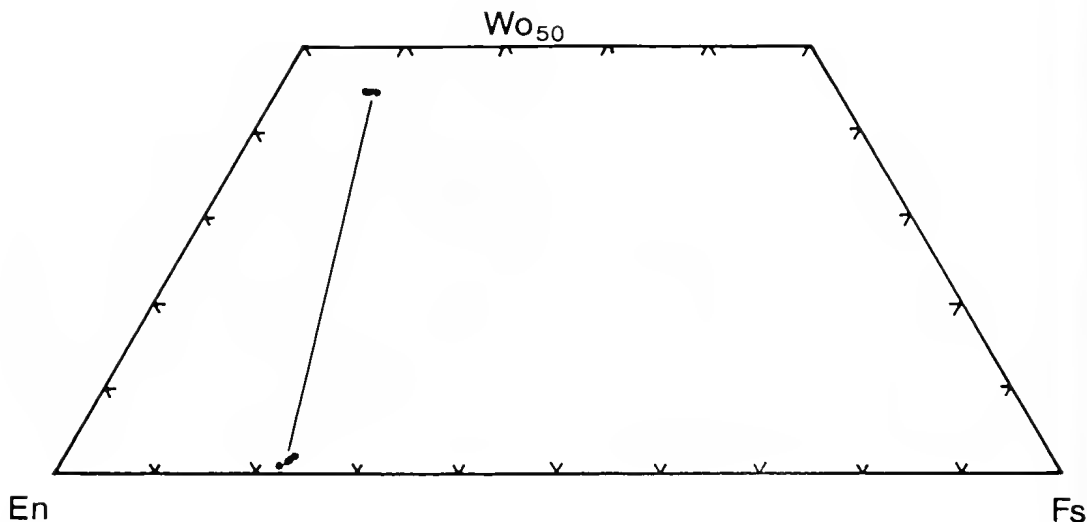
Fig. 5. Pyroxene quadrilateral showing compositions of the orthopyroxene and clinopyroxene in the Bealiba Meteorite.

pink grains up to 2.5 mm. Chromite is widespread as rounded pale grey grains up to about 0.1 mm across. Thin concretionary rims to kamacite grains consist of goethite, which also occurs as small skeletal grains and microveinlets in the groundmass. These features are a result of breakdown of the metallic minerals during weathering.

Microprobe analysis of various grains of kamacite and taenite showed compositional ranges represented by Fe/Ni = 14–17 and Fe/Ni = 1.9–2.7 (wt% basis) respectively. Cr contents were below detectable limits. The chromite contains small amounts of Al, Ti and Mg (Table 1). Chlorine-bearing areas associated with the Fe-rich alteration around kamacite grains suggest the presence of akaganéite (Buchwald & Clarke 1989).

CLASSIFICATION

A full chemical analysis of the Bealiba meteorite was not carried out but the meteorite can be classified on textural and mineralogical grounds. Summarising the criteria for chondrite classification based on Dodd (1981) and Van Schmus & Wood (1967), the Bealiba meteorite has: homogeneous olivine ($Fo_{75}Fa_{25}$) and pyroxene compositions; an orthorhombic low-Ca pyroxene; feldspar forming distinct groundmass and interstitial grains, and with composition $Ab_{83}An_{11}Or_6$; chondrules ranging from distinct to poorly defined; a matrix which is relatively

coarse-grained and recrystallised; and distinct kamacite and taenite grains. On these grounds, the Bealiba meteorite is best classified as an L6 chondrite.

CONCLUSION

Meteorite discoveries are uncommon in Victoria, although ironically the fall of the rare carbonaceous chondrite at Murchison in September 1969 is one of the best-documented and most spectacular of all known meteoritic events. Bealiba is only the tenth Victorian meteorite described (Henry 1988, Fitzgerald 1980) and the second L6 chondrite. The first L6 chondrite, the Kulnine Meteorite, is a single stone of 55 kg collected on Kulnine Station west of Mildura around 1886 (Walcott 1916). It has some unusual chemical and textural features suggestive of higher than usual crystallisation temperatures and possible "shock" recrystallisation (Mason 1973). Based on the 300 km separation of their discovery sites and their different features, the Bealiba and Kulnine meteorites represent distinct fall events.

ACKNOWLEDGEMENTS

obtained copies of title plans for Bealiba township. Microprobe analyses were obtained in the Department of Geology, University of Melbourne, with the assistance of Pat Kelly. Brian Mason (Smithsonian Institution, Washington, DC) kindly provided information on the Kulnine meteorite.

REFERENCES

BUCHWALD, V. F. & CLARKE, R. S. JR., 1989. Corrosion of Fe–Ni alloys by Cl-containing akaganéite (β–FeOOH): the Antarctic meteorite case. *American Mineralogist* 74: 656–667.

DODD, R. T., 1981. *Meteorites. A Petrologic- Chemical Synthesis.* Cambridge University Press.

FITZGERALD, M. J., 1980. The Oberon Bay Meteorite. *Proceedings of the Royal Society of Victoria* 91: 67–71.

HENRY, D. A., 1988. Meteorites. In *Geology of Victoria,* J. G. Douglas & J. A. Ferguson, eds, Geological Society of Australia, Victorian Division, Melbourne, 602.

MASON, B., 1973. Notes on Australian meteorites. *Records of the Australian Museum* 29: 169–181.

VAN SCHMUS, W. R. & WOOD, J. A., 1967. A chemical-petrologic classification for the chondritic meteorites. *Geochimica et Cosmochimica Acta* 31: 745–765.

WALCOTT, R. H., 1915. Descriptions of the Victorian meteorites, with notes on obsidianites. *Memoirs of the National Museum of Victoria* 6: 3–66.

THE EFFECT OF THE GRAZING GASTROPOD *BEMBICIUM NANUM* ON RECOLONIZATION OF ALGAE ON AN INTERTIDAL ROCK PLATFORM

HAL BRALEY[1], TREVOR A. ANDERSON[1,3] AND G. P. QUINN[2]

[1]Department of Biological Sciences, Deakin University, Geelong, Victoria 3217
[2]Department of Botany and Zoology, Monash University, Clayton, Victoria 3168
[3]Address for reprints

BRALEY, H., ANDERSON, T. A. & QUINN, G. P., 1991:06:30. The effect of the grazing gastropod *Bembicium nanum* on recolonization of algae on an intertidal rock platform. *Proceedings of the Royal Society of Victoria* 103 (1): 13–16. ISSN 0035-9211.

The predominant organisms found in the littoral zone of a rock platform at Aireys Inlet, Victoria, were surveyed in autumn 1989. The predominant algal species was the brown alga *Hormosira banksii*, while the predominant invertebrate herbivore was *Bembicium nanum*. The abundances of *H. banksii* and *B. nanum* were negatively correlated. *B. nanum* had a significant effect on recolonization of the ephemeral brown alga *Scytosiphon lomentaria* but there was no effect on recolonization of *H. banksii* or of the green alga *Enteromorpha intestinalis*.

MANY RECENT studies have described the structure of intertidal communities (Cubit 1984, Lubchenco 1980, 1983, Lubchenco & Cubit 1980, Underwood 1980, 1984, Underwood & Jernakoff 1981). Many of these studies have shown that the structure of an intertidal algal community is affected by both the physical environment (including such factors as immersion) and by grazing, which may eliminate algae above a certain level on the shore (Jernakoff 1983, Steneck 1982, Underwood 1980). Whilst many experiments have examined competition between intertidal herbivores (Fletcher & Creese 1985, Fletcher & Underwood 1987, Quinn & Ryan 1989, Underwood 1984), relatively few have examined specific algal-herbivore interactions (Hunter & Hunter 1983, Underwood 1980, Underwood & Jernakoff 1981) and fewer still have been conducted in Victoria.

An initial survey of a rocky intertidal platform at Aireys Inlet, Victoria, showed a significant negative correlation between the density of the littorinid snail *Bembicium nanum* and the abundance of the predominant algal species *Hormosira banksii*. Previous studies have observed that this littorinid snail grazes micro and ephemeral algae (Quinn & Ryan 1989, Underwood 1980, 1984). A study was conducted to examine the effects of the presence of *B. nanum* upon the recolonisation of *H. banksii* and two species of ephemeral algae, *Enteromorpha intestinalis* and *Scytosiphon lomentaria*.

STUDY SITE AND METHODS

The study site was a sandstone and clay intertidal platform located at Aireys Inlet, Victoria. The platform extends from the sublittoral zone to the high water mark.

Initial Survey

An initial study was conducted to determine the abundance and total number of algae and herbivores present. Twenty one-metre square quadrats were selected randomly and the organisms within the quadrats counted. Correlation analyses were then performed between the number of plants present and the number of herbivores (Zar 1984).

Major Study

Twenty areas each measuring 200×200 mm were randomly selected over the rock platform. The substratum within these areas was cleaned to bare rock by scraping with a metal implement and scrubbing vigorously with a domestic scrubbing brush. The experimental areas were then bounded by a layer of antifouling paint (25% $CuSO_4$). Nineteen *B. nanum* (the maximum density of *B. nanum* found) were placed into each of 10 areas (inclusion) whilst all benthic herbivores were excluded from the remaining 10 areas (exclusion).

The enclosures were monitored weekly (or as close as tides and weather would permit) for

eight weeks between mid April and early June 1989. On each visit, where necessary, animals were replaced in test areas. The number of plants and algal species were recorded at each visit, and colour photographs were taken at fortnightly intervals to aid analysis of algal abundance. Variation in the mass of organic material in each experimental area was determined at the end of the experimental period. The central four centimetre square portion of each experimental area was scraped with a razor blade and the scrapings dried at 50° C for 24 hours. After weighing to the nearest 0.1 mg, the scrapings were ashed at 550° C for 24 hours and re-weighed. The loss in weight was attributed to organic matter. Analysis of variance was performed on log-transformed plant numbers and on log-transformed dry weights of organic matter found after 8 weeks in test versus control area.

RESULTS

Initial Survey

Table 1 shows the abundance of predominant organisms in the littoral zone of the rock platform. The alga *Hormosira banksii* was the predominant species, covering 100% of the substratum in the lower zones, but becoming patchy

Species	Mean	SE
Hormosira banksii	159.0	32.8
Ulva lactuca	2.8	1.2
Corallina spp.	1.2	0.8
Siphonaria diemenensis	63.9	17.2
Austracochlea constricta	3.7	1.4
Bembicium nanum	98.8	28.5

Table 1. Abundance of predominant organisms found on the rock platform (number of organisms present/ m^2, n = 20).

and sparse in the higher zones. Small amounts of *Ulva lactuca* and *Corallina* spp. were found but no *Scytosiphon lomentaria* or *Enteromorpha intestinalis* were found in this survey. The most numerous herbivore present was *B. nanum*, averaging 98.8 animals/m^2 and reaching densities up to 473 animals/m^2 in some areas. The pulmonate limpet *Siphonaria diemenensis* was also found in large numbers. A significant negative correlation was recorded between *H. banksii* and *B. nanum* (r = -0.705, df = 18, P < 0.001). No other significant correlations were found.

Major Study

The ephemeral species *S. lomentaria* and *E. intestinalis* were the dominant recolonising algae
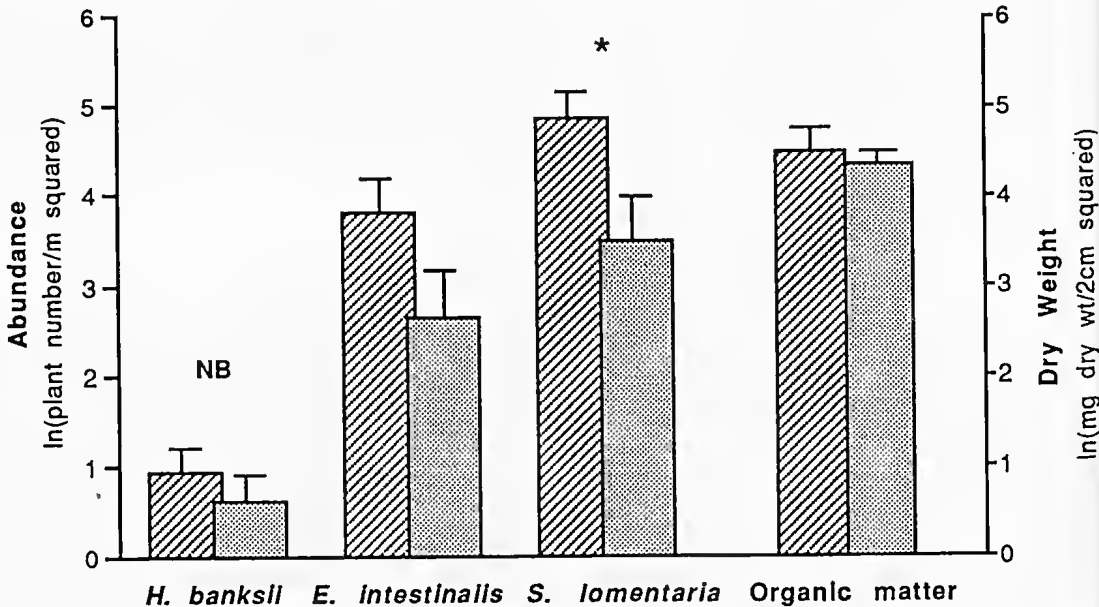

Fig. 1. Abundance of algae and dry weight of organic matter after 8 weeks following clearing of experimental areas in inclusion (diagonal rule) versus exclusion (stipple) areas. NB, analysis of *H. banksii* not performed due to the large number of null values; * = significant value of p (p < 0.05); inclusion = areas containing *B. nanum*; exclusion = areas where *B. nanum* excluded.

found during this experiment, covering 80–100% of the substratum in control areas and approximately 50% in test areas (those containing *B. nanum*) after 8 weeks growth (Fig. 1). Over the experimental period, *H. banksii* regrowth was greatest after 3 weeks; subsequently the number of *H. banksii* plants decreased.

The results of the analysis of variance show that *B. nanum* exhibited a significant (F = 5.90; df = 1,18; p = 0.026) inhibition on the recolonisation of *S. lomentaria*. No significant effect of *B. nanum* upon *E. intestinalis* (F = 3.15; df = 1,18; P = 0.084) recolonisation or upon total organic matter (F = 0.2; df = 1,18; P = 0.646) was seen in this experiment. Insufficient numbers of *H. banksii* were found in the recolonisation experiment for analysis.

DISCUSSION

In this study *B. nanum* exhibited a significant negative effect on the recolonisation of *S. lomentaria* over the intertidal platform during the period mid April to early June. This phenomenon may also indirectly alter the recolonisation of other species of algae (Lubchenco 1983, Underwood 1980, Underwood and Jernakoff 1981). It has been previously noted (Quinn & Ryan 1989, Underwood 1980, 1984) that *B. nanum* grazes on ephemeral algae, such as *Ulva* spp., and on microalgae. Quinn & Ryan (1989) also observed *B. nanum* grazing upon *E. intestinalis* and *S. lomentaria* in a study conducted during winter and spring, but no evidence was given that *B. nanum* is able to restrict numbers of colonizing *S. lomentaria*.

In the present study, no direct significant effects of *B. nanum* upon *E. intestinalis* or *H. banksii* were observed. It is feasible, however, that grazers may reduce the numbers of the most competitively aggressive algal species. An initial recolonisation of the perennial *H. banksii*, which subsequently became overgrown by the opportunistic ephemeral species *S. lomentaria* and *E. intestinalis*, suggests that grazing gastropods such as *B. nanum* may enhance the recolonisation of *H. banksii* over a longer period. Despite the reduction in the number of *S. lomentaria* in areas where *B. nanum* was present, no significant reduction of total organic matter was observed. Since the organic matter was measured in the central region of each experimental area, this latter result may reflect the patchy nature of the recolonisation of the algae rather than an effect of grazing. A longer study may clarify these points.

Experimental areas were bounded by a layer of antifouling paint (adjusted to 25% CuSO₄). The toxic effects of copper are believed to repel gastropods and prevent them from crossing a barrier of such paint (Cubit 1984). Antifouling paint was used in preference to cages in order to alleviate cage effects such as a reduction in wave and wind action, shading and harbouring of water and food particles (Cubit 1984, Underwood 1980). These microclimatic changes may also be compounded by the growth of algae on cages and by the presence of roofs on cages (Underwood 1980). Antifouling paint did not prevent *B. nanum* leaving the enclosures, and missing animals were replaced when necessary, although no *B. nanum* entered the control areas. Loss of animals from test areas was greater in the lower zones and may have been due to increased wave action and immersion in these zones.

In conclusion, *B. nanum* has been seen to exert a significant effect over the recolonisation of the ephemeral brown alga *Scytosiphon lomentaria* in the late autumn to early winter period in Victoria. *B. nanum* thus plays a recognizable role in the structure of this intertidal community.

ACKNOWLEDGEMENTS

REFERENCES

CUBIT, J. D., 1984. Herbivory and the seasonal abundance of algae on a high intertidal rocky shore. *Ecology* 65: 1904–1917.

FLETCHER, W. J. & UNDERWOOD, A. J., 1987. Interspecific competition among subtidal limpets: effects of substratum heterogeneity. *Ecology* 68: 387–400.

FLETCHER, W. J. & CREESE, R. G., 1985. Competetive interactions between co-occurring herbivorous gastropods. *Marine Biology* 86: 183–191.

HUNTER, R. D. & RUSSELL-HUNTER, W. D., 1983. Bioenergetic and community changes in intertidal Aufwuchs grazed by *Littorina littorea*. *Ecology* 64: 761–769.

JERNAKOFF, P., 1983. Factors affecting the recruitment of algae in a midshore region dominated by barnacles. *Journal of Experimental Marine Biology and Ecology* 67: 17–31.

LUBCHENCO, J., 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. *Ecology* 61: 333–344.

LUBCHENCO, J., 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* 64: 1116–1123.

LUBCHENCO, J. & CUBIT, J. O., 1980. Heteromorphie life histories of certain marine algae as adaptions to variations in herbivory. *Ecology* 61: 676–687.

QUINN, G. P. & RYAN, N. R., 1989. Competitive interactions between two species of intertidal herbivorous gastropods from Victoria. Australia. *Journal of Experimental Marine Biology and Ecology* 125: 1–12.

STENECK, R. S., 1982. A limpet coralline alga association. Adaptions between a selective herbivore and its prey. *Ecology* 63: 507–522.

UNDERWOOD, A. J., 1980. Effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. *Oecologia* (Berlin) 46: 201–213.

UNDERWOOD, A. J., 1984. Vertical and seasonal patterns in competition for microalgae between intertidal gastropods. *Oecologia* (Berlin) 64: 211–222.

UNDERWOOD, A. J. & JERNAKOFF, P., 1981. Effects of interactions between algae and grazing gastropods on the structure of a low shore intertidal community. *Oecologia* (Berlin) 48: 221–233.

ZAR, J. H., 1984. *Biostatistical Analysis*, 2nd edn, Engleworth Cliffs: Prentice Hall.

GALAXIAS BREVIPINNIS GÜNTHER (PISCES, GALAXIIDAE) IN NORTH-EASTERN VICTORIA: FIRST RECORDS FOR THE MURRAY–DARLING DRAINAGE BASIN

A. K. MORISON AND J. R. ANDERSON

Kaiela Fisheries Research Station, Flora and Fauna Division,
Department of Conservation & Environment, PO Box 1226,
Shepparton, Victoria 3632

MORISON, A. K. & ANDERSON, J. R., 1991:06:30. GALAXIAS BREVIPINNIS Günther (Pisces, Galaxiidae) in north-eastern Victoria: first records for the Murray–Darling drainage basin. *Proceedings of the Royal Society of Victoria* 103 (1): 17–28. ISSN 0035-9211.
During surveys in 1990, *Galaxias brevipinnis* Günther, 1866 was caught at 11 sites in two catchments in north-eastern Victoria, the first reports of this species from the Murray–Darling drainage basin. Data on gonad maturity stage, gonadosomatic index and maximum oocyte diameter indicate that the species has established breeding populations that spawn in April or early May. Assessment of past survey results indicates that these populations are most probably recently introduced rather than being undiscovered natural populations. Movement of *G. brevipinnis* from the upper Snowy River catchment through tunnels carrying water for hydro-electric and irrigation purposes is regarded as the most likely means of introduction but other possibilities are discussed. Specimens were collected from several types of stream habitat including rocky fast-flowing habitats and one site with fine sediments and slow flow. Occurrence of the species was independent of the presence of *Salmo trutta* L. The spread of *Galaxias brevipinnis* may adversely affect other aquatic species indigenous to the Murray–Darling drainage basin.

THE FAMILY Galaxiidae contains about 40 species of small salmoniform fishes of the Southern Hemisphere including 22 species from southern Australia (Allen 1989). Galaxiids constitute a major proportion of the total number of freshwater fish species native to southern Australia (McDowall & Frankenberg 1981). However, only three species of galaxiids are included among the list of about 31 species of native freshwater fish found in the Murray-Darling Basin, the largest drainage basin in Australia. Those three species are the mountain galaxias, *Galaxias olidus* Günther, 1866, the flat-headed galaxias, *G. rostratus* Klunzinger, 1872, and the diadromous common galaxias, *G. maculatus* (Jenyns, 1842) (Anderson 1989, Pierce 1989).

In Australia, *G. brevipinnis* Günther, 1866 is found in coastal drainages from Sydney to Adelaide, and in Tasmania; it is also found in New Zealand, the Chatham Islands, and the Auckland and Campbell Islands (McDowall 1980b). It is a relatively large, elongate fish known to reach 278 mm, with thick, fleshy fins and usually with a distinct blue-black patch above the base of the pectoral fin (McDowall 1980b). It is usually found in small, clear-flowing, forested streams, where it often inhabits rocky areas with fast-flowing water, and in lakes where it is reported as either living among rocks on the lake bed or evenly distributed throughout the body of water (Andrews 1976, McDowall 1980b). *G. brevipinnis* is an amphidromous species having a marine "whitebait" juvenile stage in New Zealand, Tasmania and on the Australian mainland, although this is believed to be a facultative rather than obligatory phase to its life-cycle (McDowall & Frankenberg 1981). Spawning is believed to take place in streams in autumn or early winter (Koehn & O'Connor 1990); newly-hatched young go to sea for several months and return when 45–50 mm long (McDowall 1980b). However, many land-locked populations have been reported from lakes in New Zealand and Tasmania, and from one lake on the Australian mainland (McDowall & Frankenberg 1981).

G. brevipinnis has not been recorded previously from the Murray–Darling system (Allen 1989), although it is present in coastal streams on the Fleurieu Peninsula in South Australia near the mouth of the River Murray (McDowall & Frankenberg 1981). In this paper we document the first records of *G. brevipinnis* from the Murray–Darling Basin and discuss the possible reasons for the species' newly discovered presence.

METHODS

Map grid references, stream names, altitudes (from the 1:100,000 National Topographic Map

Series) and dates of sampling at the 50 sites sampled (Figs 1 and 2) are given in the Appendix.

On 26 January 1989 and 21 March 1990 single-wing fyke nets (mesh size 25 mm and funnel opening 200 mm) were used in Koetong Creek (site 31). During the more intensive survey between 23 March and 1 June 1990 a shore-mounted, pulsed DC electrofisher (H. Riddle 1KWC model) powered by a Honda portable generator (model EG 1900X, maximum output 1.9 KVA) was used. At most sites, a stream section about 100 m long was sampled; shorter sections were sampled when access was limited or a large number of fish were caught. We maximised our chances of finding populations of *G. brevipinnis* by sampling small streams with rocky substrates, often in the headwaters of catchments, although ease of access also determined eventual sampling sites.

Descriptions given by McDowall (1980a), Cadwallader & Backhouse (1983) and Merrick & Schmida (1984) were used to identify specimens, but all *Galaxias* specimens and a representative sample of other native species were preserved for confirmation of identity. Specimens were fixed in 10% neutralised formalin for a minimum of 3 days and then transfered for one day to 40% ethanol, then to 60% ethanol, and finally they were preserved in 70% ethanol. The standard length of each preserved *G. brevipinnis* specimen was measured to the nearest 1 mm with dial callipers, and weights of whole fish and their gonads were measured to the nearest 0.01 g on a Mettler PE3600 digital balance. The gonads of each *G. brevipinnis* specimen were examined macroscopically and their maturity stage was estimated according to the scheme used by Humphries (1989): Stage I, virgin; Stage II, recovering spent; Stage III, developing; Stage IV, mature; Stage V, ripe; Stage VI, spent. As a further indication of the stage of gonad development, the gonadosomatic index (GSI) was calculated as weight of gonad/total weight of fish × 100. Maximum oocyte diameters were measured with an eyepiece micrometer on a Zeiss stereomicroscope at 40 × magnification. Data on size and reproductive condition of female *G. brevipinnis* collected at sites surveyed during 21–30 March were combined, as were data on females collected during May 1990. Data on size and reproductive condition of males collected during 23–29 March 1990 were combined, as were those for males collected during 28 May – 1 June 1990.

The number of vertebrae, excluding hypural centra, of *G. brevipinnis* from north-eastern Victoria were counted on x-ray negatives taken of the preserved specimens in the Ichthyology Department, Museum of Victoria. The significance of differences in these vertebral counts among populations of *G. brevipinnis* was tested using a single factor analysis of variance followed by a Newman–Keuls multiple range test (Zar 1974). Data for other populations of *G. brevipinnis* in Australia were obtained from McDowall & Frankenberg (1981, Table 1). Only populations with data from 10 or more specimens were used in the analysis.

To test whether the frequencies of occurrence of *G. brevipinnis*, *G. olidus* and *S. trutta* were independent of each other, we tested 2×2 contingency tables by using the chi-square test with the Yates correction for continuity (Zar 1974).

Information on the known distribution of *G. brevipinnis*, records of other species of *Galaxias* from the survey area, and locations surveyed in the past were obtained from Tunbridge (1978), McDowall & Frankenberg (1981), Cadwallader & Backhouse (1983), Brumley et al. (1987), and Koehn & O'Connor (1990). In addition, the collections of the Australian Museum, Sydney, and the Museum of Victoria, Melbourne, were checked for all records of *Galaxias* species in the upper Murray, Kiewa, upper Murrumbidgee and upper Snowy River catchments. Unpublished records from surveys by the Victorian Fisheries Division (Baxter 1985, 1988, 1989, 1990 and pers. comm., and Cadwallader pers. comm.) were also checked.

All preserved specimens of *G. brevipinnis* and

Date	Sex	Standard Length (mm)		Maturity Stage (n)				GSI (%)		Max. Oocyte Diameter (mm)	
		mean	range	II	III	IV	Total	mean	range	mean	range
21–30 March	Females	98	78–137	2	0	10	12	11.6	0.28–18.8	1.10	0.08 –1.40
28–31 May	Females	124	85–150	2	3	0	5	0.61	0.36– 0.99	0.37	0.16–0.76
23–29 March	Males	89	75–114	0	1	6	7	11.4	4.32–17.3		
28 May–1 June	Males	86	67–113	3	1	2	6	3.59	0.14–11.8		

Table 1. Size and reproductive condition of female and male *G. brevipinnis* collected between 21 March and 1 June 1990.
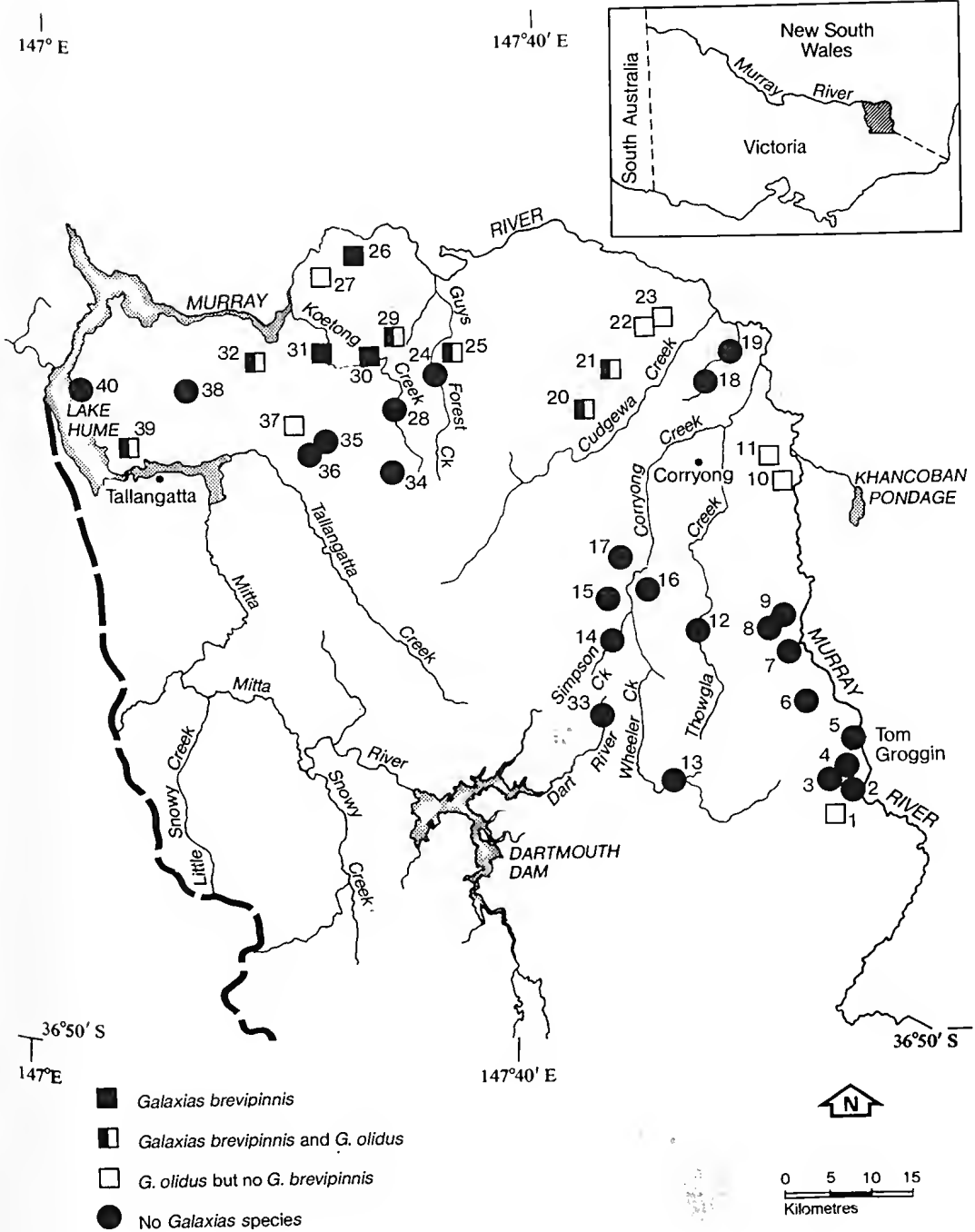
Fig. 1. Sampling sites in north-eastern Victoria upstream of Hume Dam showing locations where *Galaxias brevipinnis* and *G. olidus* were caught (January 1989–June 1990). Details of site locations and other fish species caught are given in the appendix.
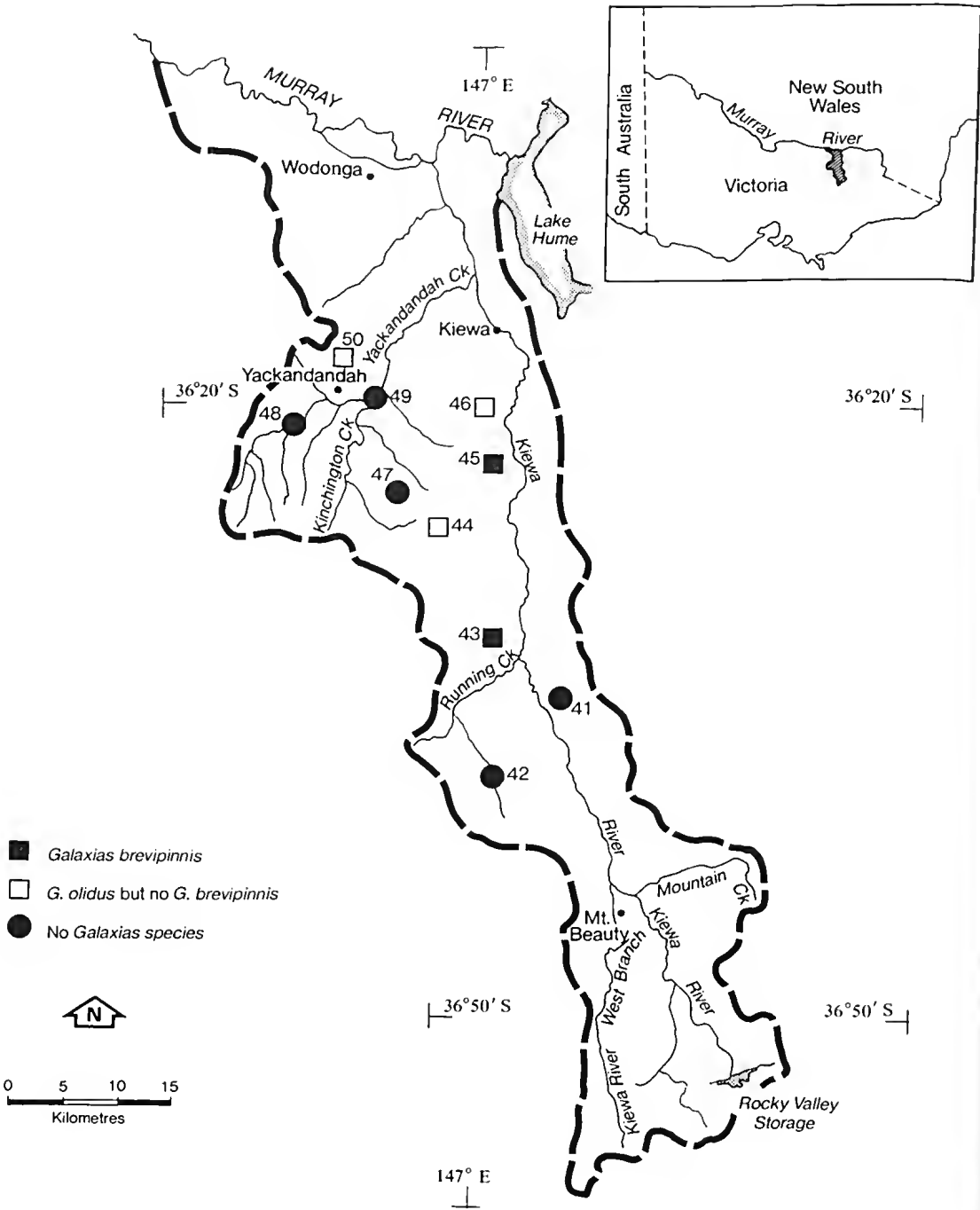
Fig. 2. Sampling sites in the Kiewa River catchment showing locations where *Galaxias brevipinnis* and *G. olidus* were caught (May–June 1990). Details of site locations and other fish species caught are given in the appendix.

G. olidus have been lodged at the Museum of Victoria.

RESULTS

The numbers of each fish species caught at each of the 50 sites sampled between 21 March and 1 June 1990 are given in the Appendix. *G. brevipinnis* was caught at 11 sites, nine of which were in the catchment of the upper River Murray and two in the catchment of the Kiewa River (Figs 1 and 2).

Distribution of G. brevipinnis

On 26 January 1989 three specimens of *G. brevipinnis* were collected from one rocky pool in Keotong Creek (site 31). The only other species of fish collected from this site were the exotic brown trout, *Salmo trutta,* and rainbow trout,*Oncorhynchus mykiss,* although the two-spined blackfish, *Gadopsis bispinosus,* was recorded 2 km downstream below a series of falls. On 21 March 1990 another specimen of *G. brevipinnis* was collected at site 31 and three more specimens from further upstream (site 30). Between 23 March 1990 and 1 June 1990 *G. brevipinnis* were recorded at nine sites extending from Jarvis Creek near Tallangatta (site 39) upstream to an unnamed tributary of Cudgewa Creek, 13 km north-west of Corryong (site 20, Fig. 1). Five of these sites were in small streams draining directly into Lake Hume and four sites were in small streams draining directly into the River Murray or its tributaries.

Because these results indicated that *G. brevipinnis* was widely distributed in the catchment of the Hume Weir, sampling was extended to the catchment of the Kiewa River, the first major tributary entering the River Murray below the weir. *G.brevipinnis* was recorded from two of the ten sites sampled on tributaries of the lower reaches of the Kiewa River (Fig. 2).

G. brevipinnis was caught at sites within an altitude range of 210–530 m; the range for all sites was 210–790 m. At sites where *G. brevipinnis* was caught streams ranged from the very small (widths less than 1 m; maximum depths about 300 mm (sites 20, 43)) to larger (widths 5 m; maximum depths of pools more than 2 m (site 31)). These sites, like most sites we selected, frequently had rock and boulder substrates, but *G. brevipinnis* was also recorded at one site (site 45) where the substrate was predominantly sand and finer sediment and where the stream flowed comparatively slowly.

Riparian vegetation at the sites where *G. brevipinnis* was caught ranged from essentially undisturbed native vegetation (sites 29–31, 43) to introduced grasses on grazing land (site 39) or introduced trees (site 45). *G. brevipinnis* was also caught in pools in the headwater sections of intermittent streams which became subterranean further downstream (sites 26, 39).

Co-habiting species

G. olidus was found at 16 sites, including six sites (sites 20, 21, 25, 29, 32 and 39) where *G. brevipinnis* was also caught. A chi-square test of the 2 × 2 contingency table indicated that the presence of *G. brevipinnis* was independent of the presence of *G. olidus* ($X^2 = 2.079$, $p > 0.05$).

Salmo trutta was found with *G. brevipinnis* at five sites (Sites 30, 31, 39, 43, and 45), with *G. olidus* at four sites (Sites 1, 10, 37, 39) and alone at 23 other sites.Chi-square tests indicated that the presence of *S. trutta* had a significant effect on the presence of *G. olidus* ($X^2 = 8.621$, $P < 0.01$) but that the presence of *G. brevipinnis* was independent of the presence of *S. trutta* ($X^2 = 0.862$, $P > 0.05$).

The only other species of fish found with *G. brevipinnis* were *Gadopsis bispinosus* (site 21) and *Oncorhynchus mykiss* (sites 30, 31, and 43). Other species recorded during the surveys were freshwater blackfish, *Gadopsis marmoratus* (sites 4, 12 and 38), southern pigmy-perch, *Nannoperca australis* (site 46) and redfin, *Perca fluviatilis* (site 37).

Reproductive condition

Comparisons of the maturity stages, GSI and maximum egg diameters for *G. brevipinnis* collected in March, May and June indicate that spawning had taken place in April or early May. In samples collected later the proportion of fish with more mature gonads (Stage IV) was smaller, mean GSI values for both females and males were much lower, and the maximum size of oocytes was also much smaller. These differences are not due to differences in the size of fish caught in the two time periods: the later samples contained more larger female fish, and the mean size and the size range of males were similar (Fig. 3, Table 1). Between these sampling periods water temperatures were falling and stream flows had substantially increased following rainfall over the area in mid-April. After further heavy rainfall, sampling on 17–18 May was curtailed because high water velocities and high
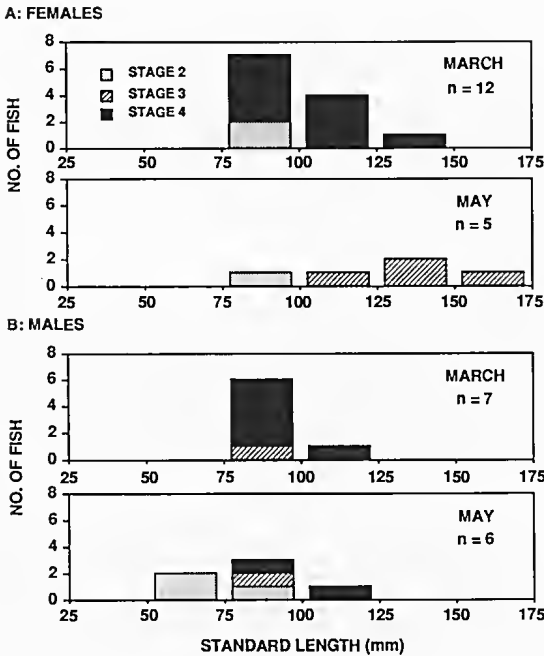
A: FEMALES

B: MALES

STANDARD LENGTH (mm)

Fig. 3. Length–frequency histograms showing maturity stage for (A) female and (B) male *Galaxias brevipinnis* caught in March and May 1990.

turbidity made efficient electrofishing imposs-ible.

Vertebral morphology

An analysis of variance of the mean number of vertebrae of *G. brevipinnis* in our samples and in 10 of those studied by McDowall & Frankenberg (1981) showed significant differences among the samples (F = 17.85, P < 0.001). However, a Newman–Keuls test could not separate samples into distinct groups.

DISCUSSION

Our survey results indicate that populations of *G. brevipinnis* are present at 11 sites in nine streams in catchments in north-eastern Victoria. Moreover the distribution of the 11 sites, the size range of *G. brevipinnis* we caught and their reproductive condition suggest that the species has been present for several years at least and has established breeding populations that spawn in April or early May. The populations reported here may be part of the natural range of the species, and perhaps remnants of a once wider distribution within the Murray–Darling Basin,

or they may be recently established popu-lations.

Pre-1989 surveys

Fish surveys carried out prior to 1989 at 89 sites in the Upper Murray catchment and 29 sites in the Kiewa River catchment recorded no speci-mens of *G. brevipinnis*, suggesting that the species has recently extended its range into the Murray–Darling drainage basin. These surveys included multiple samples from all major tribu-taries and were widely distributed between their headwater and lowland sections. Sampling methods included dip-netting (27 sites), electro-fishing (4 sites), fyke nets (5 sites), and the use of the piscicide rotenone (77 sites). The surveys recorded *Galaxias* spp. at 35 sites, including both *G. olidus* (32 sites) and *G. rostratus* (3 sites near Albury). We expect that *G. brevipinnis,* if present in the area, would also have been caught even though none of the pre-1989 sampling sites coincided exactly with sites where we caught *G. brevipinnis.*

It is possible that *G. brevipinnis* was caught during these earlier surveys but was not correctly identified. However, all the specimens in the Museum of Victoria have been recently exam-ined by T. Raadik (formerly of the Museum's Department of Ichthyology) who found no *G. brevipinnis* among the many collections of *G. oli-dus* from north-eastern Victoria. Specimens of *G. olidus* reported from north-eastern Victoria by McDowall & Frankenberg (1981) were care-fully examined by those authors and they re-ported no *G. brevipinnis.* Species of *Galaxias* recorded during Fisheries Division surveys have not always been unambiguously identified but no specimens of *G. brevipinnis* have been col-lected. Small specimens of *Galaxias* can be dif-ficult to identify in the field but, because *G. brevipinnis* grows much larger than *G. olidus* and *G. rostratus* (the only other galaxiids known to inhabit the same area), the larger specimens are readily distinguishable. Presumably *G. brevi-pinnis* would have been correctly identified among the larger specimens.

Murray–Darling populations

The April–May spawning period indicated for *G. brevipinnis* in north-eastern Victoria is within the autumn or early winter spawning period pre-viously reported for *G. brevipinnis* in mainland Australia (Frankenberg 1969, Koehn & O'Con-nor 1990), Tasmania (Andrews 1976) and New

Zealand (McDowall 1970). However, land-locked (and usually lacustrine) populations of normally diadromous galaxiids frequently exhibit shifts in spawning period and migration patterns compared with riverine populations and migrate upstream in spring to spawn in streams (Pollard 1971, Andrews 1982, Humphries 1989). Populations of *G. brevipinnis* in north-eastern Victoria are effectively land-locked because of their distance from the sea (2,225 km from Lake Hume to the mouth of the River Murray) and because of the barriers impeding a return migration of juvenile fish. It is not known whether larvae of *G. brevipinnis* in north-eastern Victoria move downstream after hatching as do those in coastal streams, but such a movement would lead them eventually to Lake Hume (or Lake Mulwala for Kiewa River populations). Consequently, recruitment probably depends on juveniles which remain upstream of Lake Hume. Regular recruitment from the Snowy catchment or from the Murray seems unlikely. *G. brevipinnis* has not yet been found in Lake Hume and details of any migratory movements of these populations are unknown.

Origin of parent stock

G. brevipinnis from South Australian populations near the mouth of the River Murray may have moved upstream into north-eastern Victoria, but such a movement would have involved an upstream migration of more than 2,000 km, past two large dams (Yarrawonga Weir and Hume Dam) and 13 smaller weirs. It seems improbable that such a migration would be successful in recent times but not during the thousands of years prior to European settlement. Moreover, if such a movement had occurred we would expect that *G. brevipinnis* would have been found in other tributaries entering the River Murray further downstream.

It is more plausible that *G. brevipinnis* was deliberately or inadvertently released into the catchment of the upper River Murray. We do not regard *G. brevipinnis* as a natural part of the fish fauna of north-eastern Victoria. There are several potential sources and modes of introduction for the *G. brevipinnis* now found in this area (and these origins are not mutually exclusive).

Consignments of trout from hatcheries within the natural range of *G. brevipinnis* have been released into streams in the upper Murray, and these consignments may have included some specimens of *G. brevipinnis*. The species may have been illegally stocked into streams, other

public waters or private waters from which escape occurred. Specimens of *G. brevipinnis* may also have been transported inland for aquarium specimens or as live bait and escaped into the wild. Evidence for any of these events is lacking.

The most likely route by which *G. brevipinnis* gained access to north-eastern Victorian waters is via the Snowy Mountains Scheme by which water is diverted from the upper Snowy River catchment to the upper River Murray for irrigation and the generation of hydro-electricity (Fig. 4). *G. brevipinnis* has been recorded at sites in the upper Snowy River catchment, including the Snowy River below Eucumbene Dam (McDowall & Frankenberg 1981; collected 1973, J. Paxton pers. comm.), and four creeks draining to Lake Eucumbene (Tilzey 1976, as *G. coxii = G. brevipinnis*).

Snowy Mountains Scheme

The volume of water diverted annually by the Snowy Mountains Scheme is about 580 GL, but this volume may almost double in dry years and comprise about one-third of the total inflow to Lake Hume (Jacobs 1989). Some of the water flows by gravity from the Island Bend Pondage on the upper Snowy River to the Geehi Reservoir in the River Murray catchment through the 14.4 km-long Snowy–Geehi tunnel (Fig. 4). Additional water flows by gravity from Lake Eucumbene to the same tunnel via the 23.5 km-long Eucumbene–Snowy Tunnel, or is pumped from Lake Jindabyne via the 9.9 km long Jindabyne–Island Bend Tunnel (Snowy Mountains Hydro-electric Authority 1982). Fish would have little difficulty moving through these tunnels: screens on tunnel entrances are large relative to fish size, and the tunnel gradients are generally small (flow can be in either direction in some tunnels depending on levels in the storages).

The rock wall of Geehi Dam (slope 2:1 and vertical height difference between full supply level and dam crest of 5.49 m) would not be a significant barrier to *G. brevipinnis* gaining access to the river downstream. The species is noteworthy for its ability to climb steep waterfalls and moist rocky faces by using its pectoral and pelvic fins, and to move great distances inland past formidable barriers (McDowall & Frankenberg 1981).

Another route by which *G. brevipinnis* or other species of fish could move into the Murray–Darling drainage basin is via the Eucumbene–
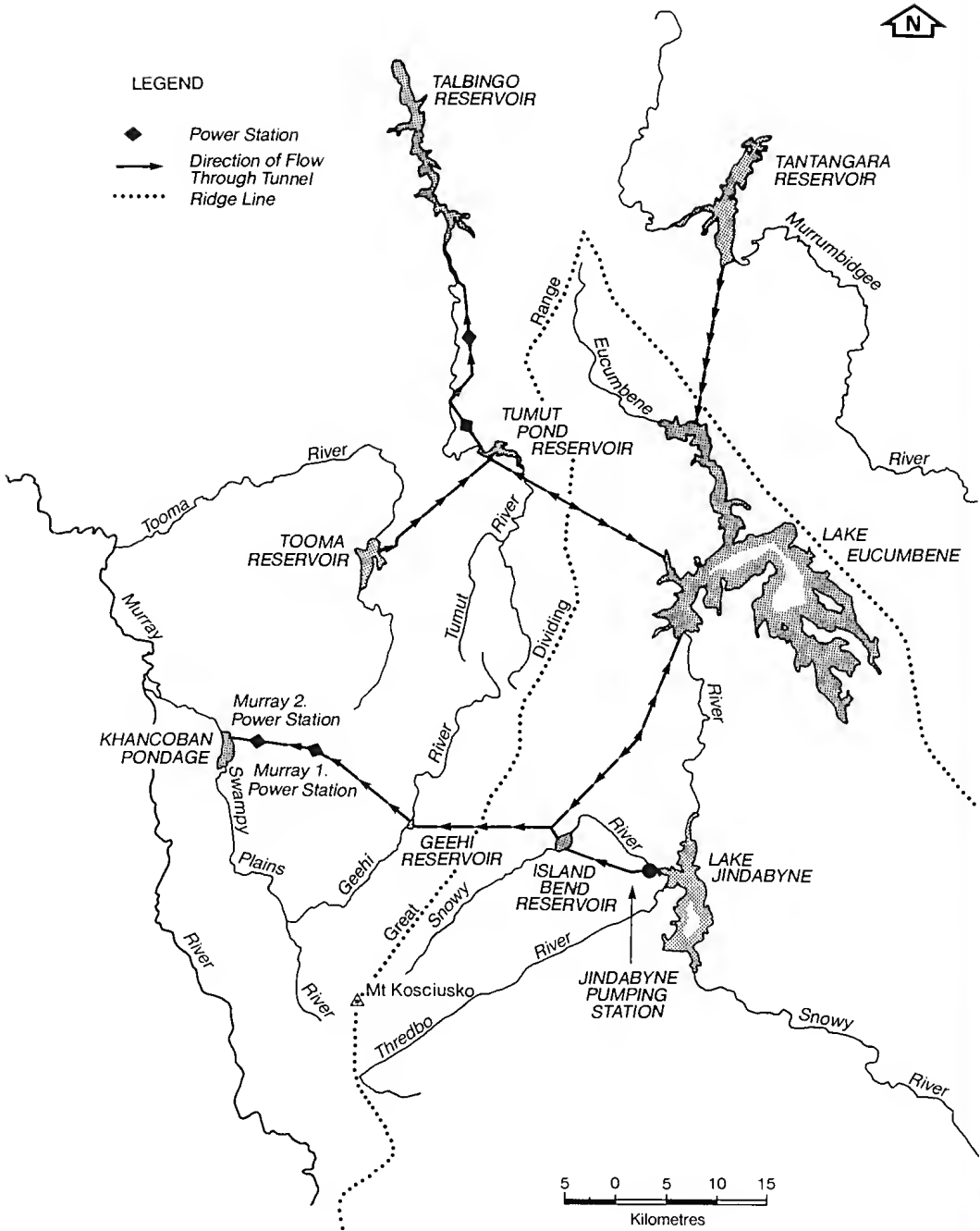
Fig. 4. Map of the Snowy Mountains area showing routes for diversions of water between catchments.

Tumut Pond Tunnel (Fig. 4). Conversely, the Tantangara–Eucumbene connection could provide fish access from the Murray–Darling catchment to the Snowy River catchment.

Vertebral morphology

Evidence for the source of the parent stock of *G.brevipinnis* populations may be obtained from the vertebral morphology of specimens. McDowall & Frankenberg (1981) reported a trend among populations of *G. brevipinnis* for an increasing number of vertebrae with increasing latitude. The frequency distribution of the number of vertebrae in *G. brevipinnis* from north-eastern Victoria (Fig. 5) has a higher mode than that of other populations in Victoria, South Australia or New South Wales and most closely resembles those of more southerly populations in Tasmania and New Zealand. Although the differences are not significant and there is a need for more specimens to be analysed, the data suggest that the north-eastern Victorian population may be unlike those in South Australia and New South Wales. The distribution may be characteristic of the parental stock but may have been influenced by environmental factors during development, by the random effects of a population bottleneck during the early colonisation phase, or by sampling bias. No other morphological characteristics of *G.brevipinnis* allow different populations to be differentiated (McDowall & Frankenberg 1981).
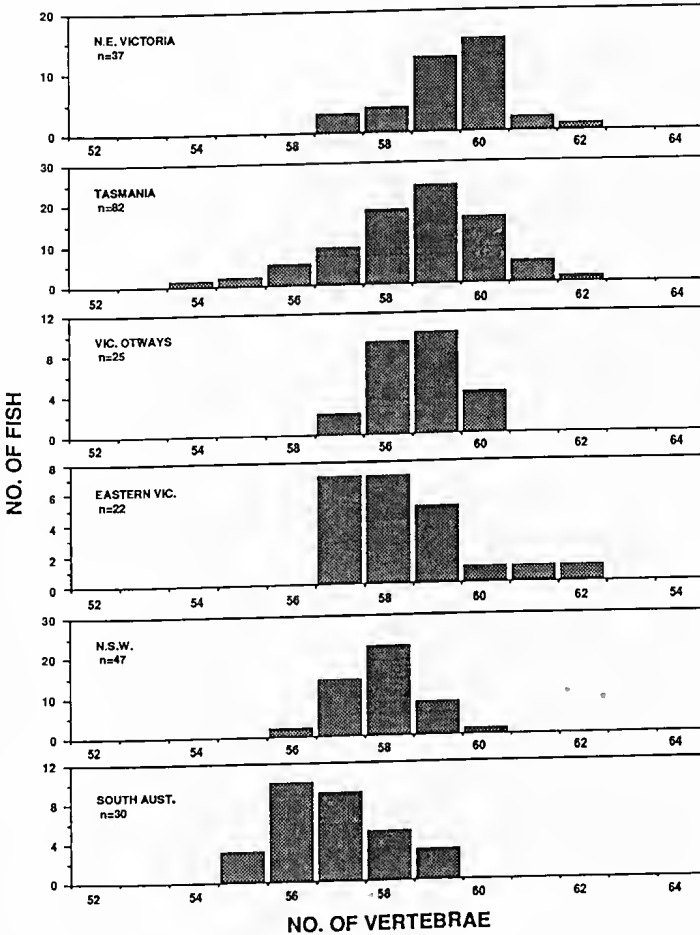

Fig. 5. Frequency distributions of number of vertebrae in *Galaxias brevipinnis* from north-eastern Victoria and from localities listed in McDowall & Frankenberg (1981).

Further work

Biochemical methods of examining variation among populations of *G. brevipinnis*, such as electrophoresis and mitochondrial DNA analysis, may provide more conclusive evidence as to the source of populations in north-eastern Victoria and therefore indicate the likely mechanism of their introduction.

The introduction of *G. brevipinnis* to streams in north-eastern Victoria may lead to increased competition with indigenous species, in particular *G. olidus*. *G. brevipinnis* and *G. olidus* normally do not occur together in coastal streams (McDowall & Frankenberg 1981), although recent surveys in the Otways region recorded *G. brevipinnis* at two of the three sites at which *G. olidus* occurred (Koehn & O'Connor 1990). There has been some concern that *G. brevipinnis* has expanded its range in Tasmania at the expense of other galaxiid species (W. Fulton, Inland Fisheries Commission, Tasmania, pers. comm). Other species of fish such as *Gadopsis bispinosus*, which are not naturally sympatric with *G. brevipinnis*, may also be adversely affected by this addition to the local fish fauna.

Further work will be needed to clarify the source, status and reproductive cycle of populations of *G. brevipinnis* in north-eastern Victoria. Further survey work may record additional populations in the Murray–Darling Basin, would allow any potential expansion of known populations and the response of indigenous species to be monitored, and could also identify key features of the life cycle of this normally amphidromous species.

ACKNOWLEDGEMENTS

REFERENCES

ALLEN, G. R., 1989. *Freshwater Fishes of Australia*. TFH Publications, Brookvale, Australia, 240 p.

ANDERSON, J. R., 1989. Status of fish – issues and discussion points. In *Proceedings of the Workshop on Native Fish Management, Canberra, 16–17 June 1988*, Murray–Darling Basin Commission, Canberra, 1–6.

ANDREWS, A. P., 1976. A revision of the family Galaxiidae (Pisces) in Tasmania. *Australian Journal of Marine and Freshwater Research* 27: 297–349.

ANDREWS A. P., 1982. A Tasmanian landlocked population of the normally diadromous fish *Galaxias maculatus* (Jenyns). *Papers and Proceedings of the Royal Society of Tasmania* 116: 85–90.

BAXTER, A. F., 1985. *Trout management group fish population surveys, 1978–1985: location of sampling sites and fish species caught*. Arthur Rylah Institute for Environmental Research Technical Report Series No. 15, Department of Conservation, Forests and Lands, Victoria, Melbourne, 41 p.

BAXTER, A. F., 1988. *A summary of trout management group fish population surveys 1987*. Fisheries Management Report No. 21, Freshwater Fish Management Branch, Department of Conservation, Forests and Lands, Victoria, Melbourne.

BAXTER, A. F., 1989. *A summary of trout management group fish population surveys 1988*. Fisheries Management Report No. 27, Freshwater Fish Management Branch, Department of Conservation, Forests and Lands, Victoria, Melbourne.

BAXTER, A. F., 1990. *A summary of trout management group fish population surveys 1989*. Fisheries Management Report No. 31, Freshwater Fish Management Branch, Department of Conservation, Forests and Lands, Victoria, Melbourne.

BRUMLEY A. R., MORISON A. K. & ANDERSON J. R., 1987. *Revision of the conservation status of several species of warmwater native fish after surveys of selected sites in northern Victoria (1982–1984)*. Arthur Rylah Institute for Environmental Research Technical Report Series No. 33, Department of Conservation, Forests and Lands, Victoria, Melbourne, 93 p.

CADWALLADER, P. L. & BACKHOUSE, G. N., 1983. *A Guide to the Freshwater Fish of Victoria*. Government Printer, Melbourne, 249 p.

FRANKENBERG, R. S. A., 1969. Studies on the evolution of galaxiid fishes with particular reference to the Australian fauna. PhD thesis, University of Melbourne.

HUMPHRIES, P., 1989. Variation in life history of diadromous and landlocked populations of the spotted galaxias, *Galaxias truttaceus* Valenciennes, in Tasmania. *Australian Journal of Marine and Freshwater Research* 40: 501–518.

JACOBS, T. A., 1989. Regulations of the Murray–Darling River System. In *Proceedings of the Workshop on Native Fish Management, Canberra, 16–17 June 1988*, Murray–Darling Basin Commission, Canberra, 55–98.

KOEHN, J. D. & O'CONNOR, W. G., 1990. Distribution of freshwater fish in the Otway region, south-western Victoria. *Proceedings of the Royal Society of Victoria* 102: 29–39.

McDOWALL, R. M., 1970. The galaxiid fishes of New Zealand. *Bulletin of the Museum of Comparative Zoology Harvard University* 139: 341–431.

McDOWALL, R. M. (ed.), 1980a. *Freshwater Fishes of South-Eastern Australia.* Reed Books, Sydney, 208 p.

McDOWALL, R. M., 1980b. Family Galaxiidae. Galaxiids. In *Freshwater Fishes of South-Eastern Australia*, R. M. McDowall, ed., Reed Books, Sydney, 79–81.

McDOWALL, R. M. & FRANKENBERG, R. S., 1981. The galaxiid fishes of Australia (Pisces: Galaxiidae). *Records of the Australian Museum* 33(10): 605 p.

MERRICK, J. R. & SCHMIDA, G. E., 1984. *Australian Freshwater Fishes.* John R. Merrick, Sydney, 409 p.

PIERCE, B. E., 1989. Improving the status of our River Murray fishes: a discussion paper on the potential of co-operative management. In *Proceedings of the Workshop on Native Fish Management, Canberra, 16–17 June 1988*, Murray–Darling Basin Commission, Canberra, 7–18.

POLLARD, D. A., 1971. The biology of the landlocked form of the normally catadromous salmoniform fish *Galaxias maculatus* (Jenyns) 1. Life cycle and origin. *Australian Journal of Marine and Freshwater Research* 22: 91–123.

SNOWY MOUNTAINS HYDRO-ELECTRIC AUTHORITY, 1982. *Engineering Features of the Snowy Mountains Scheme*, 2nd edn, 167 p.

TILZEY, R. D. J., 1976. Observations on interactions between indigenous Galaxiidae and introduced Salmonidae in the Lake Eucumbene catchment, New South Wales. *Australian Journal of Marine and Freshwater Research* 27: 551–564.

TUNBRIDGE, B. R., 1978. A survey of fish populations in the Mitta Mitta River and tributaries before construction of Dartmouth Dam. In *Dartmouth Dam Project Report on Environmental Studies. Part 2, Reports.* State Rivers and Water Supply Commission for the River Murray Commission.

ZAR, J. H., 1974. *Biostatistical Analysis.* Prentice-Hall, Englewood Cliffs, New Jersey, 620 p.

APPENDIX

Date of survey, location, altitude and numbers of each fish species caught at each sample site. Basin 01E is the River Murray catchment upstream of the Mitta Mitta River, Basin 01W is the Mitta Mitta catchment, and Basin 02 is the Kiewa River catchment. P = species recorded at site on preliminary survey on 28 March 1990; Trib. = unnamed tributary.

SITE NO.	DATE	LOCATION	BASIN NO.	MAP NO.	GRID REF.	ALTI-TUDE	*Galaxias brevipinnis*	*G. olidus*	*Gadopsis marmoratus*	*G. bispinosus*	*Nannoperca australis*	*Salmo trutta*	*Oncorhynchus mykiss*	*Perca fluviatilis*
1	16.5.90	Buckwong Ck.	01E	8524	009520	550	·	1	·	·	·	2	·	·
2	16.5.90	Murray R. Trib	01E	8524	005544	570	-	-	-	-	-	-	-	-
3	16.5.90	Boggy Ck.	01E	8524	977550	600	-	-	-	-	-	4	-	-
4	16.5.90	Omeo Ck.	01E	8524	993571	540	-	-	-	-	-	3	1	-
5	16.5.90	Stony Ck.	01E	8525	002613	600	-	-	-	-	-	5	1	-
6	15.5.90	Surveyors Ck.	01E	8525	943663	550	-	-	-	-	-	12	12	-
7	15.5.90	Lt. Bunroy Ck.	01E	8525	926723	380	-	-	-	-	-	12	-	-
8	15.5.90	Ironpot Ck.	01E	8525	902736	520	-	-	-	-	-	9	-	-
9	15.5.90	Bunroy Ck.	01E	8525	907752	500	-	-	-	-	-	12	-	-
10	15.5.90	Biggara Ck.	01E	8525	905847	340	-	1	-	1	-	8	-	-
11	15.5.90	Murray R. Trib.	01E	8525	905905	360	-	24	-	-	-	-	-	-
12	18.5.90	Thowgla Ck.	01E	8425	827766	440	-	-	3	-	-	4	4	-
13	17.5.90	Cattlemans Ck.	01E	8424	786553	790	-	-	-	-	-	9	2	-
14	17.5.90	Simpson Ck.	01E	8425	703717	510	-	-	1	-	·.	12	7	-
15	30.5.90	Boyd Ck	01E	8425	698767	480	-	-	-	1	-	4	34	-
16	18.5.90	Star & Jones Ck.	01E	8425	745796	400	-	-	-	-	-	2	-	-
17	30.5.90	Rawes Ck	01E	8425	730845	300	-	-	-	-	-	16	3	-
18	18.5.90	Horse Ck.	01E	8425	818037	500	-	-	-	-	-	-	-	-
19	18.5.90	Horse Ck.	01E	8425	850060	260	-	-	-	-	-	-	-	-
20	28.5.90	Cudgewa Ck Trib.	01E	8425	685995	420	4	25	-	-	-	-	-	-
21	28.5.90	Stony Ck	01E	8425	690061	430	2	6	-	6	-	-	-	-
22	30.5.90	Pine Mountain Ck	01E	8425	753097	440	·	69	-	-	-	-	-	-
23	30.5.90	Pine Mountain Ck	01E	8425	766113	340	-	106	-	-	-	-	-	-
24	29.3.90	Burrowye Ck.	01E	8425	487047	400	-	-	-	-	-	5	-	-
25	29.3.90	Jones Ck.	01E	8425	496072	320	12	3	-	-	-	-	-	-
26	30.3.90	Flaggy Creek	01E	8325	404156	410	1	-	-	-	-	-	-	-
27	29.5.90	Stockyard Ck	01E	8326	354167	290	-	26	-	-	-	-	-	-
28	28.3.90	Koetong Ck.	01E	8325	440985	580	-	-	-	-	-	18	-	-
29	29.5.90	Jimmey Ck	01E	8325	432065	530	2	69	-	-	-	-	-	-

SITE NO.	DATE	LOCATION	BASIN NO.	MAP NO.	GRID REF.	ALTI-TUDE	C A T C H							
							Galaxias brevipinnis	G. olidus	Gadopsis marmoratus	G. bispinosus	Nannoperca australis	Salmo trutta	Oncorhynchus mykiss	Perca fluviatilis
30	23.3.90	Koetong Ck.	01E	8325	401049	470	3	-	-	-	-	1	15	-
31	21.3.90	Koetong Ck.	01E	8325	352064	280	1	-		-	-	2	2	-
32	27.3.90	Cottontree Ck.	01E	8325	276035	240	5	29	-	-	-	-	-	-
33	17.5.90	Dart R.	01W	8425	697625	740	-	-	-	-	-	5	1	-
34	28.3.90	Dry Forest Ck.	01W	8325	424907	720	-	-	-	-	-	-	-	-
35	29.5.90	Dry Forest Ck	01W	8325	372958	320	-	-	-	-	-	5	-	-
36	28.3.90	Dry Forest Ck.	01W	8325	358953	290	-	-	-	6	-	2	7	-
37	29.5.90	Kangaroo Ck	01W	8325	313974	240	-	5	-	P	-	2	P	5
38	27.3.90	George's Ck.	01W	8325	220012	320	-	-	13	-	-	-	-	-
39	27.3.90	Jarvis Ck.	01W	8325	147944	210	1	2	-	-	-	1	-	-
40	27.3.90	Bethanga Ck.	01W	8325	067006	190	-	-	-	-	-	-	-	-
41	01.6.90	Bay Ck	02	8324	105507	340	-	-	-	-	-	17	-	-
42	01.6.90	Running Ck	02	8324	014460	380	-	-	-	-	-	21	10	-
43	01.6.90	House Ck	02	8324	008586	380	1	-	-	-	-	1	5	-
44	31.5.90	Glen Ck	02	8325	947665	400	-	-	-	-	-	28	-	-
45	31.5.90	Hellhole Ck	02	8225	005744	260	3	-	-	-	-	2	-	-
46	01.6.90	Gap Ck	02	8325	009799	220	-	7	-	-	1	-	-	-
47	31.5.90	Kinchington Ck Trib.	02	8225	924751	360	-	135	-	-	-	-	-	-
48	31.5.90	Nine Mile Ck Trib.	02	8225	821773	360	-	-	-	-	-	10	1	-
49	31.5.90	Yackandandah Ck	02	8225	912817	250	-	-	-	-	-	3	-	-
50	31.5.90	Basin Ck	02	8225	870840	300	-	76	-	-	-	-	-	-

AUSTRALASIAN TERTIARY BRACHIOPODA.
THE SUBFAMILY ANAKINETICINAE NOV.

J. R. RICHARDSON

Museum of Victoria, 285–321 Russell Street, Melbourne, Victoria 3000

Four new endemic brachiopod genera (*Adnatida, Aliquantula, Elderra, Pilkena*) and
seven new species (*Anakinetica breva, A. recta, A. tumida, Magadinella hamiltonensis, Pil-
kena compressa, Adnatida gnangarensis* and *Elderra toorlooensis*) are described from Ter-
tiary bryozoan sands in Victoria, South Australia and Western Australia. The taxa are
included in the new subfamily Anakineticinae which is erected for those Australian and New
Zealand genera formerly included in the Magadinae.

WITH the exception of the Terebratellidae (sub-families Terebratellinae, Anakineticinae nov., Bouchardiinae and Magadinae), Cainozoic articulate brachiopod families are cosmopolitan in distribution. Cainozoic members of the Terebratellidae are unknown in the northern and western hemispheres but are the principal components of the Recent brachiopod faunas in Australia, New Zealand, South America and Antarctica. In these areas, brachiopods are not rare members of the benthos, as they appear to be in other parts of the world.

The subfamily Anakineticinae nov. is an exclusively southern subfamily which apparently evolved in the biogenic sands of New Zealand and Australia during the Oligocene and Miocene. In New Zealand, a drastic reduction in the extent of shallow marine shelf environments by Late Miocene time (MacKinnon 1987) resulted in the disappearance of brachiopods specialised for these regimes, and both anakineticinid genera from that area (*Magadina, Rhizothyris*) are now extinct. In contrast, the stability of the Australian region has provided a virtually continuous record (Eocene to Recent) of anakineticinids specialised for bryozoan sands. Present day communities living in the bryozoan sands of the Australian shelf replicate those found in the Tertiary bryozoan sands, and the two communities are sometimes found in juxtaposition, as in southern Victoria, for example, where cliffs of the Aire coast border shelf waters.

Living anakineticinid species have been described in a series of papers (see Richardson 1987) which show that they are widely distributed in relation to latitude, longitude and depth, and that they possess a variety of adaptations for life in shifting bryozoan sands. These species have given a new insight into the struc-

ture and function of the pedicle, showing that it is not analagous to a stalk or stem but is a variable appendage used either to tether or to move individuals in soft sediments. Differences in the pedicle system and therefore in substrate relationships are reflected in overall shape and size, as well as in the beak and cardinalia.

Erection of a new subfamily for the Australian and New Zealand genera previously included in the Magadinae leaves the latter subfamily with four European Cretaceous genera, three of which are little known. The Australasian genera have been transferred to the Anakineticinae because they differ from *Magas*, the type genus of the Magadinae, in distribution of thickening, beak type, and in the form of the posterior surface of the cardinal process. The distribution of thickening in *Magas* indicates that the dorsal valve would have been uppermost in life and the ventral valve in contact with the underlying substrate (chalk), in contrast with the opposite orientation of austral genera. The posterior surface of the cardinal process of *Magas* is small and cup-shaped whereas in the genera attributed to the Anakineticinae it is prominent and distinctive in shape, with lateral vertical or near-vertical wings flanking a median horizontal surface (trefoil). Steinich (1968) and Johansen (1987) have remarked on the similarities between *Magas chitoniformis* and *Dalliglas nobilis* (Dallinidae) which they can separate only on the composition of the loop and density of punctae. Both *Magas* and *Dalliglas* exhibit adult loops at an early stage of the developmental sequence which is characteristic of terebratella-cean families (Richardson 1975). Family position can be determined only from the patterns of resorption evident in intermediate stages, not from early or late stages of development. Adult

loop pattern therefore does not define the family position of *Magas* which may prove to be a member of the Dallinidae

Discussion of the evolutionary derivation of members of the Anakineticinae will be included in a forthcoming paper on Australian Terebratellidae.

The material described herein is housed in the collections of the South Australian Museum (SAM), the Western Australian Museum (WAM), and the Museum of Victoria (NMV).

SYSTEMATICS

Superfamily TEREBRATELLACEA King, 1850
Family TEREBRATELLIDAE King, 1850
Subfamily ANAKINETICINAE nov.

Diagnosis. Posteriorly thickened smooth Terebratellidae with permesothyrid foramen; cardinalia consisting of socket ridges, crural bases, and a cardinal process with trefoil posterior surface.

Genera included. Anakinetica Richardson, 1987; *Adnatida* nov.; *Aliquantula* nov.; *Australiarcula* Elliott, 1959; *Elderra* nov.; *Magadina* Thomson, 1915; *Magadinella* Thomson, 1915: *Parakinetica* Richardson, 1987; *Pilkena* nov.; *Pirothyris* Thomson, 1927; *Rhizothyris* Thomson, 1915.

Distribution. Cretaceous–Recent; Australia, New Zealand.

Comments. All anakineticinid genera are posteriorly thickened with a permesothyrid foramen. They differ from one another primarily in the cardinalia: in the extent of thickening of the hinge platform, in the presence of hinge pits or of a hinge trough and, if the latter is present, in its extent.

Differential thickening is a reliable indicator of free life in living forms and a permesothyrid foramen of an inert, non-muscular pedicle (Richardson 1981a); i.e. individuals that are pediculate but are neither tethered nor fixed to the underlying substrate. The presence of a hinge trough or of pits is associated with different actions of the pedicle (Richardson 1987). In the former, the action of pedicle muscles rotates the pedicle or the shell (depending on the mass of substrate bonded with the pedicle); in the latter they push the pedicle in and out of its housing, the beak. Rotatory action is associated with a bonded pedicle and attachment of the dorsal pedicle muscles to a hinge trough. In/out action is associated with a free pedicle and attachment

of dorsal adjustor muscles to a pair of posterior hinge pits.

A hinge trough is characteristic of four of the genera and may (1) extend the full length of the platform (*Magadina*), (2) be restricted to its anterior section as a result of enlargement of the inner socket ridges and cardinal process (*Magadinella, Elderra*), or (3) be restricted to its posterior region (*Aliquantula*) by enlargement of the crural bases. Genera with hinge pits may differ in the position of the hinge platform relative to the valve surface and in shell shape and beak form, differences which, in members of living genera (*Anakinetica, Parakinetica*), are related to direction of movement and to the disposition of the pedicle processes.

Neither hinge trough nor pits are evident on the hinge platform of species of *Adnatida*. The absence of any area for attachment of the dorsal pedicle adjustor muscles is a likely indicator of atrophy or loss of the pedicle system, as are the small foramen and incurved beak also seen in these species. They would have been free-lying forms without any capacity to move and similar to some of the populations of *Neothyris lenticularis* described by Chapman & Richardson (1981) and Richardson (1981b). Species within each genus are distinguished on consistent differences in size and shape, on loop pattern, and on details of the hinge platform. Loop pattern is linked with the space available within the mantle cavity. In shells of small size and heavy thickening (*Magadina, Anakinetica recta*) the adult loop is at an early stage in the developmental sequence; i.e. with a ventral ring and wide descending branches separately attached to a high median septum. A long reflected loop without septal attachments is found in *Aliquantula* and *Elderra*, genera of moderate size and having the hinge platform smaller in relation to valve area than in *Anakinetica* and *Magadinella*. The loop is rarely recovered in its entirety but its parts and their relationship are evident during dissection.

Several Japanese species are difficult to distinguish from Australian anakineticinids. The Miocene species *Tanakura tanakura* Hatai, 1936, for example, was included by me (Richardson 1987) in the Magadinae because of its similarity to species of *Anakinetica*. The Pliocene–Recent species *Nipponithyris nipponensis* Yabe & Hatai, 1934 is also very similar to *Aliquantula insolita*. However, the adult loop of *N. nipponensis* displays double lateral connecting bands (Richardson 1975), showing that it is a member of the Dallinidae. The development

and adult loop of *T.tanakura* are unknown but the short median septum carries no evidence of connecting bands, indicating that a long reflected loop would have been present. Since a loop of this type is found as the ultimate developmental stage in all families and, since no other members of the Terebratellidae have been described from Japan, it is possible that *Tanakura* is also a dallinid genus, and the similarities in shape, size, beak and cardinalia are thus considered homeomorphies resulting from the occupation of sediments of similar type. Hatai (1940) described *T. tanakura* from coarse grained sandstones consisting of fragments of marine organisms and *N. nipponensis* from a shelf substrate of sand and shell fragments.

Genus Anakinetica Richardson, 1987

Type species. *Terebratella(?) Cumingii* Davidson, 1852 from the Recent of Australia.

Other species. *Terebratula compta* Sowerby, 1845; *A. breva* sp. nov.; *A. recta* sp. nov.; *A. tumida* sp. nov.

Occurrence. Australia; Oligocene to Recent.

Diagnosis. Sulcate. Beak suberect to straight; beak ridges sharp; symphytium wide, flat; cardinal margin straight or nearly straight. Hinge platform with posterior pits for attachment of dorsal adjustor muscles. Loop with ascending and descending branches separate or fused and with lateral connecting bands.

Comments. Species of *Anakinetica* lack a hinge trough for attachment of the dorsal adjustor muscles. The solid hinge platform, formed by fusion of the socket ridges, crural bases, and the anterior surface of the cardinal process (Richardson 1987), contains two pits which flank the posterior surface of the cardinal process. In the living species *A. cumingii* and also in *Parakinetica stewarti*, these pits serve as the sites of attachment of the dorsal adjustor muscles, and it is inferred that the pedicle of all fossil species included in the genus likewise would have been free and would have functioned in similar ratchet-like fashion.

Species of *Anakinetica* differ externally in size, outline, beak length, curvature of the cardinal margin, and in strength of sulcation. Internally they differ in the length and height of the septum, stage of loop development, and in details of the hinge platform. Two of these features appear to be linked. A short septum and a more advanced loop stage (with thin lateral connecting bands) are found in *A. compta* and *A. breva*. A long septum and wide connecting bands occur together in *A. tumida* and *A. recta*. The components of the hinge platform are fused but identifiable in *A. breva* and *A. tumida* but are not identifiable in *A. compta* and *A. recta*.

Key to species of *Anakinetica*

(based on external features only)

1.	Beak length < 0.2 × valve length	*A. breva*
—	Beak length > 0.2 × valve length	2
2.	Cardinal margin curved, beak straight	*A. recta*
—	Cardinal margin straight or nearly straight, beak suberect	3
3.	Outline trapezoid, greatest width posterior to mid-length	*A. tumida*
—	Outline ovate, greatest width at mid-length; anterior commissure strongly sulcate	*A. compta*

## Anakinetica compta (Sowerby in Strezlecki, 1845)

Fig. 1A–F

Terebratula compta Sowerby in Strezlecki 1845: 297, pl. 19, fig. 4

Terebratella compta.—Tenison-Woods 1865: 2, pl. 2, fig. 4a–c.

non *Terebratella compta.*—Etheridge 1876: 19–20, pl. 2, fig. 5a–d [= *Magadinella woodsiana* (Tate, 1880)].

non *Magasella compta.*—Tate 1880: 162–163, pl. 10, fig. 6a–c [= *A. breva* sp. nov.].

Magadina compta.—Thomson 1915: 399, fig. 10

Type material. See comments.

Measurements. (In mm.)

Specimen	Total length	Dorsal valve length	Breadth	Depth
NMV P86974	18.8	15.0	14.9	8.9
NMV P3748	19.3	14.8	14.8	9.0
NMV P86973	17.9	13.6	12.9	8.9
NMV P58903	17.8	13.6	13.8	8.9
NMV P134239	18.5	14.9	15.5	8.2
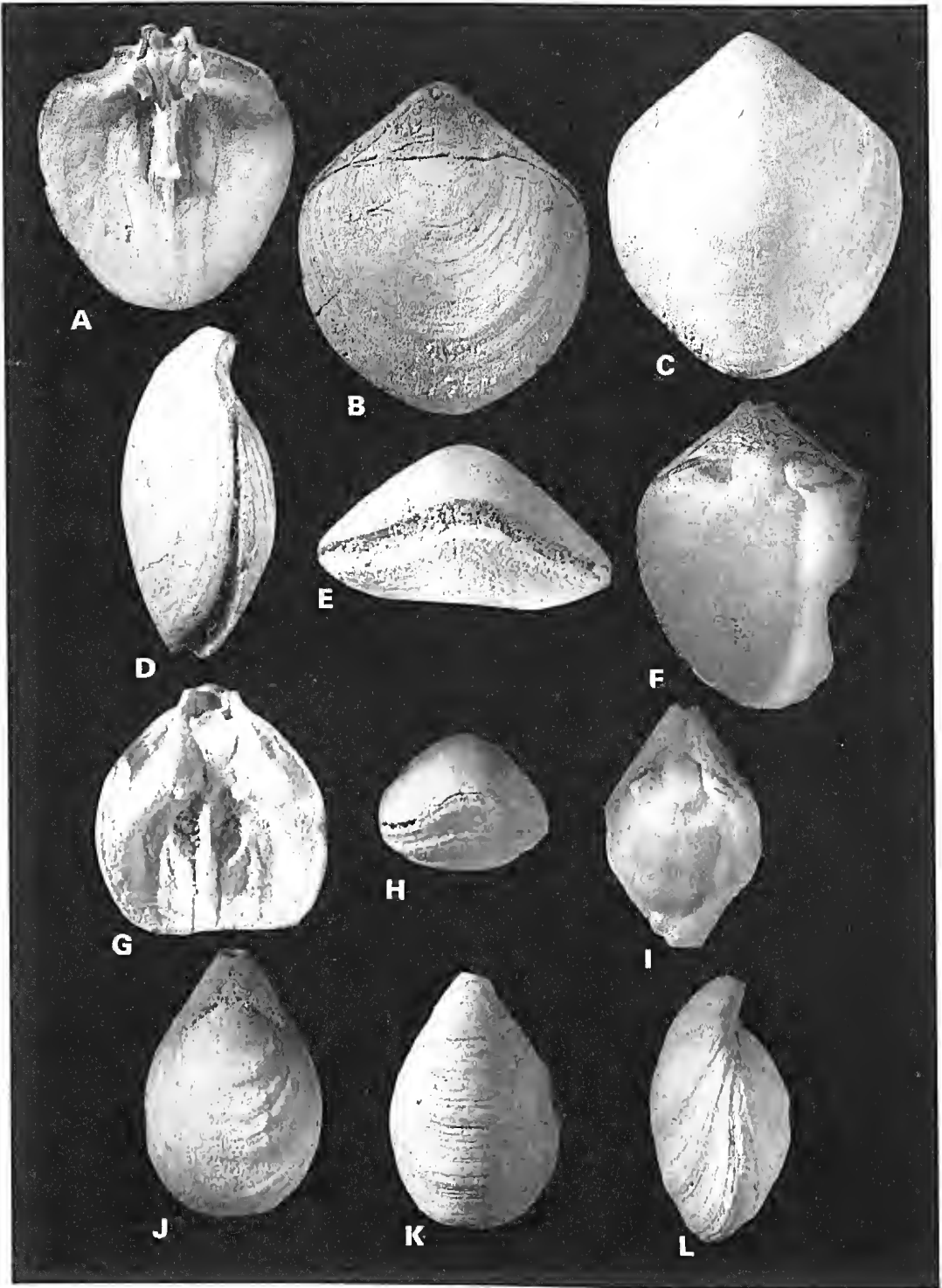
Description. Outline subquadrate, greatest width at or slightly posterior to mid-length; dorsal valve with flattened umbo; anterior commissure deeply and narrowly sulcate. Beak suberect; cardinal margin straight; symphytium wide, flat to gently concave. Hinge platform wedge-shaped, almost square with indented posterior margin; surface relief low; posterior surface of cardinal process large, lateral surfaces lining posteriorly projecting socket ridges. Medium septum thick, low, terminating mid-length of valve. Loop with thin lateral connecting bands. Hinge teeth triangular in outline. Beak interior and lateral walls heavily thickened, leaving round tunnel for pedicle.

Comments. Sowerby (in Strzlecki 1845) described *Terebratula compta* on the basis of specimens collected from "an elevated beach at Port Fairy" on the Cape Otway coast, Victoria. Tate (1880) noted that "Strzlecki mistook our Older Tertiary deposits for Post Tertiary beaches". Port Fairy (if considered as synonymous with Point Fairy) contains no Tertiary outcrops although they occur inland in this general area. In 1865, Tenison-Woods referred specimens collected at Mount Gambier and Portland to *T. compta* and his figures agree with those of Sowerby. The Natural History Museum, London, where some of Sowerby's material is deposited, has no record of *T. compta*. The specimens described and figured herein were collected from the Mount Gambier Limestone (Janjukian, Upper Oligocene) at Portland, Victoria. Since no problem exists in the identification of Sowerby's species, and in accordance with Article 75 (b)(ii) of the International Code of Zoological Nomenclature, it is not considered necessary to designate a neotype.

Anakinetica recta sp. nov.

Fig. 1G–L

Name. From Latin *rectus* (straight), in reference to the beak.

Type material. Holotype WAM 90.241 and paratypes WAM 90.242–90.246, NMV P134722, from Frank Paulik's Bore (Lot 6, depth unknown), Jandakot, Western Australia.

Other horizons and localities. Western Australia. Jandakot: Adrian's Nursery Bore at 38.4 to 39.3 m; Schafer's Bore (Lot 415) at 40.6 m; Cement Works Bore at 33.6 to 33.7 m; Poletti's Bore No. 2 (Lot 7) at 39.6 to 41.1 m; Gnangara Bore No. 8 at 77.8 m. Gosnells: Kowalski's Bore (Lot 1) at 28.4 to 29.6 m. All material cited is housed in the Western Australian Museum.

Measurements. (In mm.)

Specimen	Total length	Dorsal valve length	Breadth	Depth
WAM 90.241	9.9	8.1	7.7	4.8
WAM 90.242	9.1	7.6	6.6	4.8
WAM 90.243	9.3	7.2	6.1	4.8
WAM 90.244	9.1	7.7	6.6	5.0
NMV P134722	8.9	6.9	6.4	3.7

Description. Outline elongate-ovate with greatest width at mid-length. Beak straight, symphytium slightly concave, cardinal margin curved. Hinge platform outline trapezoidal; posterior ends of socket ridges blunt, projecting slightly beyond posterior margin of valve; boundaries of components of platform not identifiable. Median septum extending slightly beyond mid-length of valve, high anteriorly. Loop with ascending and descending branches separate, attachments to septum wide. Hinge teeth triangular in outline. Lateral walls and beak interior heavily thickened, leaving round tunnel for pedicle.

Comments. Dr G. Kendrick (pers. comm.), Western Australian Museum, considers the age of the bores to be Pliocene to Early Pleistocene.

Anakinetica tumida sp. nov.

Fig. 2A–F

Name. From Latin *tumidus* (swollen), in reference to the cardinalia.

Type material. Holotype NMV P17329 and paratypes NMV P17330, P17331, P134203–P134207, from the Brighton Sands, Cheltenham Member (Cheltenhamian, Pliocene), Beaumaris, Victoria.

Fig. 1. A–F, *Anakinetica compta* (Sowerby, 1845). A, NMV P86984, dorsal interior, × 2.5. B–E, NMV P86974, dorsal, ventral, lateral, anterior (ventral valve uppermost) views, × 2.5. F, NMV P134202, ventral interior, × 2.5. G–L, *Anakinetica recta* sp. nov. G, paratype WAM 90.245, dorsal interior, × 5. H, J–L, holotype WAM 90.241, anterior (ventral valve uppermost), dorsal, ventral, and lateral views, × 4. I, paratype WAM 90.246, ventral interior, × 4.
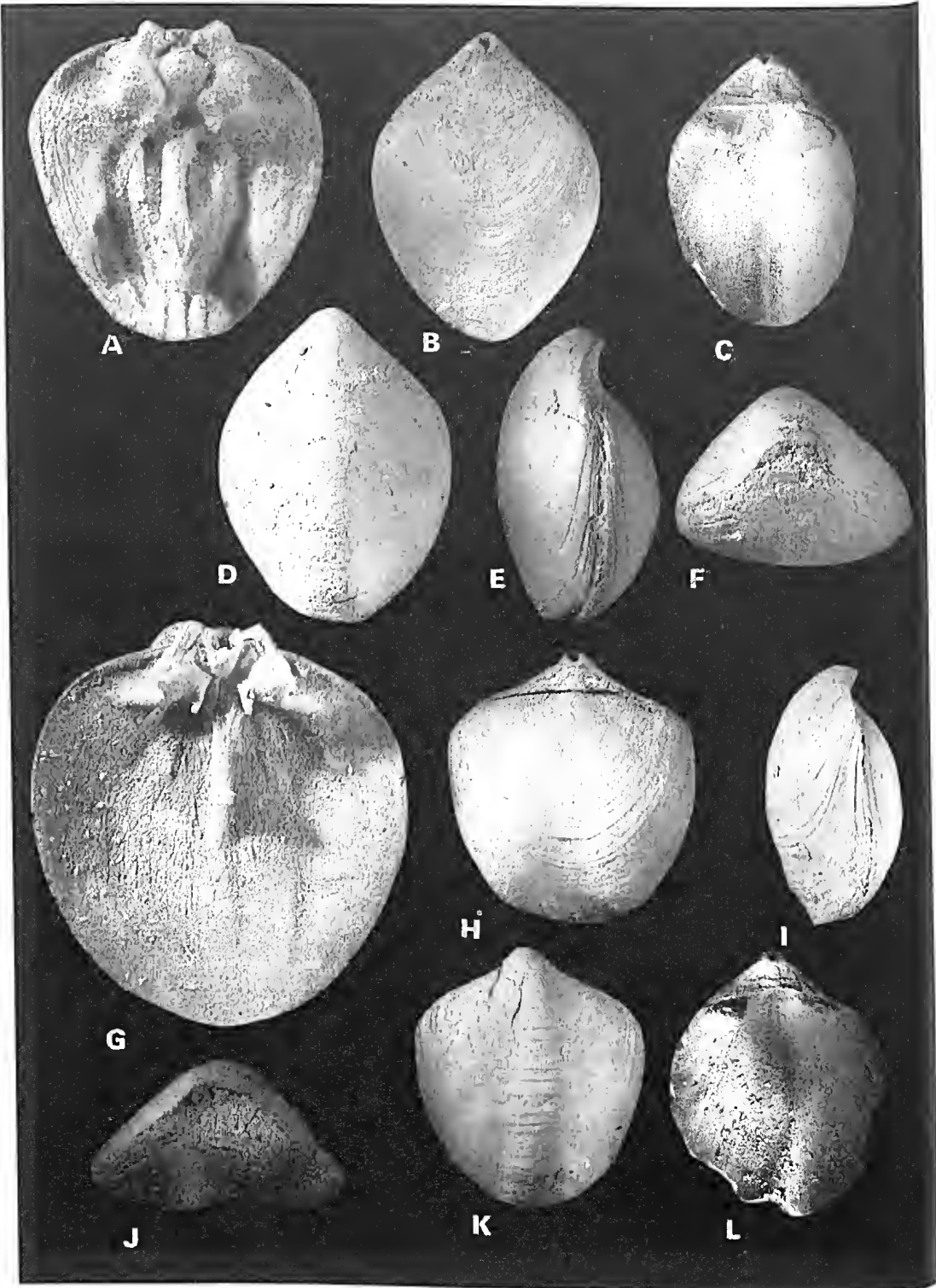
Measurements. (In mm).

Specimen	Total length	Dorsal valve length	Breadth	Depth
NMV P17329	16.8	13.2	12.4	9.2
NMV P17203	16.6	13.2	11.6	7.9
NMV P17204	17.1	13.4	12.4	9.2
NMV P17205	15.1	12.0	11.4	7.8
NMV P17206	15.0	11.9	10.8	8.1
NMV P17207	16.3	12.9	11.9	8.6

Description. Outline trapezoidal with greatest width posterior to mid-length; unequally biconvex, ventral valve deeper than dorsal valve, with median carina and steep lateral slopes; dorsal valve with flattened umbo and shallow median sulcus; anterior commissure narrowly sulcate. Beak suberect; cardinal margin straight; symphytium wide. Hinge platform outline trapezoidal; socket ridges, crural bases and anterior surface of cardinal process fused but identifiable. Median septum long, high anteriorly. Loop with ascending and descending branches having separate attachments to septum. Hinge teeth triangular in outline. Beak interior and lateral walls heavily thickened, leaving round tunnel for pedicle.

Comments. A. *tumida* closely resembles the Recent species A. *cuningii*. In A. *tumida* the cardinal margin is typically straight and variants with a slightly curved margin are rare, whereas the cardinal margin of A. *cumingii* varies from slightly to moderately curved. The ventral valve of A. *tumida* is always more strongly convex than the dorsal valve; in A. *cumingii* the valves are commonly equal in biconvexity. Fusion of the elements of the cardinalia appears to occur at a later stage in A. *tumida* than in A. *cumingii*; one dorsal valve of the former, 9 mm in length, exhibits medial fusion of the crural bases but not with the anterior surface of the cardinal process, so that a small posterior hinge trough is present at this stage.

Anakinetica breva sp. nov.

Fig. 2G–L

Magasella compta.—Tate 1880: 162–163, pl. 10,

fig. 6a–e [non *Anakinetica compta* (Sowerby in Strzelecki, 1845)].

Name. From Latin *brevus* (short), in reference to the beak length.

Type material. Holotype NMV P17348, paratypes NMV P17349, P17350, P134213–P1234216, from the Point Addis Limestone (Janjukian, Upper Oligocene), Aireys Inlet, Victoria.

Other horizons and localities. South Australia. Mannum Formation (Lower Miocene): River Murray cliffs at Mannum. Victoria. Fyansford Formation (Longfordian, Lower Miocene): North Belmont Quarry, Geelong. Puebla Formation (Longfordian Lower Miocene): Jan Juc Point, mouth of Spring Creek, Torquay. Scutellina Limestone (Longfordian, Lower Miocene): Jan Juc, Torquay. All material cited is housed in the Museum of Victoria.

Measurements. (In mm.)

Specimen	Total length	Dorsal valve length	Breadth	Depth
NMV P17348	18.0	15.8	14.9	9.1
NMV P134213	18.6	15.5	15.6	9.7
NMV P134214	17.7	15.6	16.0	9.4
NMV P134215	17.4	15.4	14.4	9.0
NMV P134216	16.1	14.0	12.8	8.6

Description. Outline ovate, greatest width slightly posterior to mid-length. Dorsal valve almost plane, umbo flattened with median sulcus. Anterior commissure deeply and narrowly sulcate. Beak suberect; cardinal margin straight. Hinge platform short, length approximately 3 mm in dorsal valve 15 mm long; outline trapezoidal; anterior surface of cardinal process prominent, fused dorsally. Median septum short, terminating posterior to mid-length. Loop with thin lateral connecting bands. Hinge teeth triangular in outline. Lateral walls and beak interior moderately thickened.

Magadinella Thomson, 1915

Type species. Magasella Woodsiana Tate, 1880 from the Upper Oligocene to Middle Miocene of Australia.

Other species. M. *mineuri* Richardson, 1987; M. *hamiltonensis* sp. nov.

Fig. 2. A–F, *Anakinetica tumida* sp. nov. A, paratype NMV P17330, dorsal interior, × 4. B, D–F, holotype NMV P17329, dorsal, ventral, lateral, and anterior (ventral valve uppermost) views, × 3. C, paratype P17331, ventral interior, × 3. G–L, *Anakinetica breva* sp. nov. G, paratype NMV P17349, dorsal interior, × 4. H–K, holotype NMV P17348, dorsal, lateral, anterior (ventral valve uppermost) and ventral views, × 2.25. L, paratype NMV P17350, ventral interior, × 2.5.

Occurrence. Australia; Upper Oligocene, Miocene, Recent.

Diagnosis. Sulcate. Beak erect to nearly straight; beak ridges sharp; symphytium wide; hinge line slightly to strongly curved. Hinge platform with shallow hinge trough, variable in size; cardinal process with swollen anterior process. Loop with ascending and descending branches fused anteriorly.

Comments. The diagnosis of the genus given by Richardson (1987) has been slightly modified following study of the two Tertiary species. The beak of the Recent species *Magadinella mineuri* is one-fifth to one-sixth the shell length, the symphytium is slightly concave without a median ridge, the cardinal margin is strongly curved, and the cardinalia occupy approximately one-third to one-quarter the length of the dorsal valve. In size and convexity *M. mineuri* and *M. woodsiana* are similar, but the cardinal margin of *M. woodsiana* may be slightly to strongly curved, a median ridge is variably developed on the symphytium, and the hinge platform is shorter relative to dorsal valve length. *M. hamiltonensis* is smaller, not heavily thickened, and the beak, hinge platform, and septum are all shorter than in the other two species.

Magadinella woodsiana (Tate, 1880)

Fig. 3A–F

Magasella Woodsiana Tate 1880: 163–164, pl. 10, fig. 3a–d.—Tate 1899: 256–257.

Magasella compta.—Pritchard 1896: 142–143 [partim., non *Anakinetica compta* (Sowerby in Strzelecki, 1945)].

Magadinella woodsiana.—Thomson 1915: 400–402, fig. 13a–e.—Thomson 1927: 277–278, fig. 92a–e.

Type material. Syntypes SAM T886A–K, M, N, from Morrundi, River Murray, South Australia. Horizon unknown.

Other horizons and localities. South Australia. Mount Gambier Limestone (Janjukian, Upper Oligocene): Mount Gambier. Victoria. Calder River Limestone (Janjukian, Upper Oligocene): Wilks' Localities 3 and 4, Aire coast. Point Addis Limestone (Janjukian, Upper Oligocene): Point Addis; Aireys Inlet; Kawarren. Sandford Limestone (Janjukian, Upper Oligocene):

quarry on south side of Runymede Road, Sandford. All material cited is housed in the Museum of Victoria.

Measurements. (In mm; specimens from the Point Addis Limestone.)

Specimen	Total length	Dorsal valve length	Breadth	Depth
NMV P17341	21.8	18.6	17.2	11.2
NMV P134223	18.0	14.0	12.1	9.9
NMV P134224	18.4	15.0	12.4	10.8
NMV P134225	17.1	14.7	11.2	11.1
NMV P134226	19.2	15.6	10.9	10.0
NMV P134227	17.4	13.9	11.5	9.8

Description. Outline variable, pyriform to ovate (narrowly to broadly) with maximum breadth at mid-length or farther forward; moderately to strongly biconvex. Beak nearly straight to suberect, one-quarter to one-eighth ventral valve length; symphytium flat to slightly concave, median longitudinal ridge variably developed; cardinal margin slightly to strongly curved. Hinge platform with hinge trough between medial borders of fused crural bases and socket ridges; cardinal process anterior surface variable in size, confined to posterior area or extending to posterior border of platform, not fused dorsally. Septum low, blade-like anteriorly, crest rounded posteriorly. Loop with ascending and descending branches fused anteriorly, separate posteriorly.

Comments. *M. woodsiana* is found in greatest abundance in the Point Addis Limestone. The preceding description is based on examination of hundreds of specimens from a single horizon and supplements Tate's description of the species from Morrundi, an area from which additional material is probably not obtainable.

Magadinella hamiltonensis sp. nov.

Fig 3G–L

Name. From the type locality.

Type material. Holotype NMV P134228 and paratypes NMV P134229–P134233, P134241, P134242, from the Muddy Creek Marl (Balcombian, Middle Miocene), Muddy Creek, Hamilton, Victoria.

Fig. 3. A–F, *Magadinella woodsiana* (Tate, 1880). A, NMV P134210, dorsal interior, × 3.5. B–D, F, NMV P17341, dorsal, lateral, anterior (ventral valve uppermost) and ventral views, × 2.5. E, NMV P134211, ventral interior, × 2.25. G–L, *Magadinella hamiltonensis* sp. nov. G, paratype NMV P134229, dorsal interior, × 5.5. H, I, K, L, holotype NMV P134228, dorsal, ventral, lateral and anterior (ventral valve uppermost) views, × 3.4. J, paratype P134230, ventral interior, × 3.4.
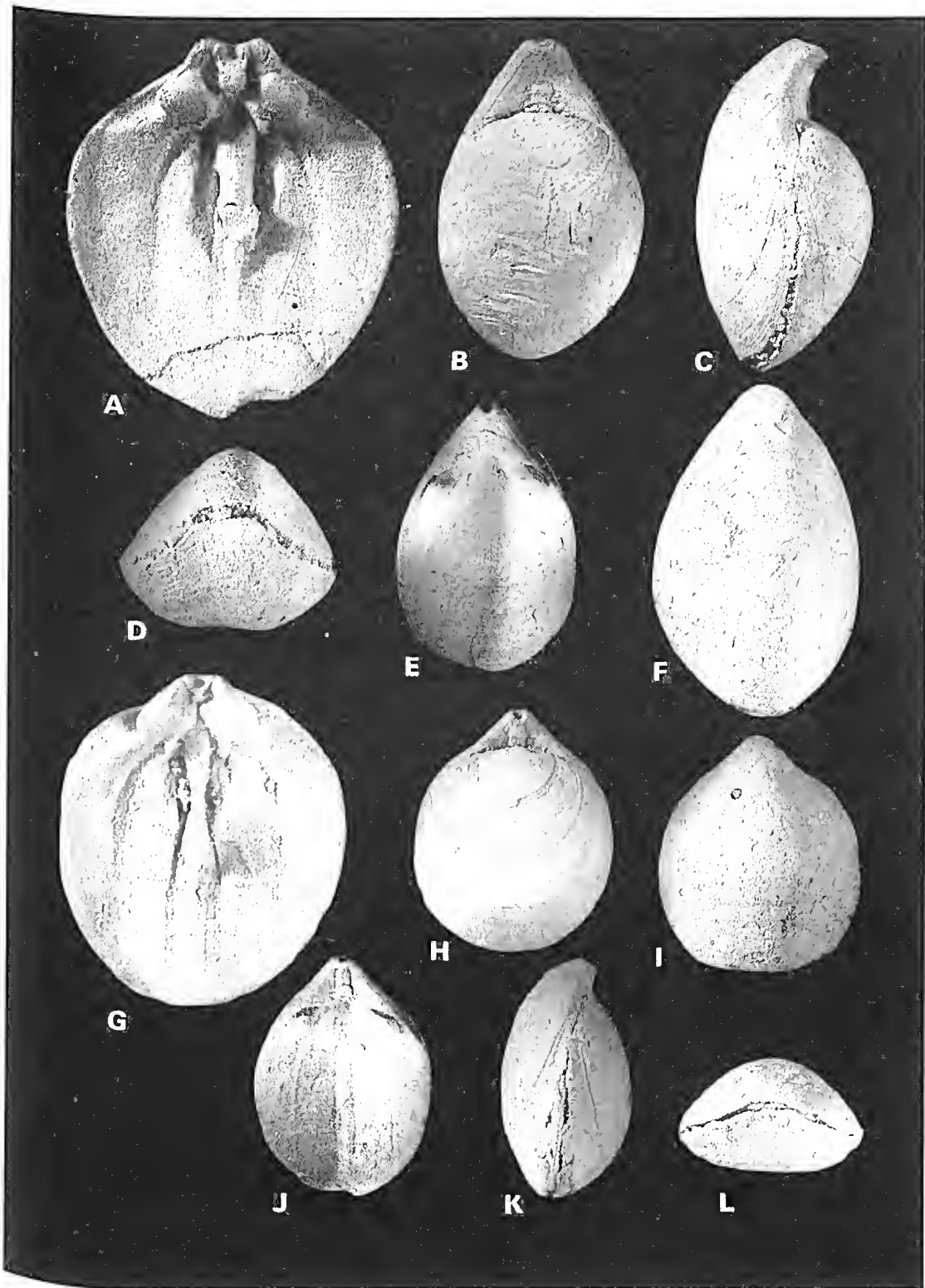
Measurements. (In mm.)

Specimen	Total length	Dorsal valve length	Breadth	Depth
NMV P134228	11.0	9.0	8.6	5.6
NMV P134231	10.3	8.9	8.6	5.6
NMV P134232	10.1	8.7	8.6	5.4
NMV P134230	10.7	8.9	8.2	5.7
NMV P134241	9.3	7.8	7.4	4.8
NMV P134242	8.4	7.6	6.5	3.9

Description. Outline ovate; moderately biconvex. Anterior commissure slightly sulcate. Beak nearly straight, approximately one-fifth of valve length; symphytium slightly concave with median longitudinal ridge; cardinal margin gently curved. Hinge platform with wide, shallow hinge trough; anterior surface of cardinal process slightly variable in size, not extending beyond posterior half of platform. Septum extending to mid-length of valve, high anteriorly. Loop with ascending and descending branches fused anteriorly.

Elderra gen. nov.

Name. From the Aboriginal (handsome). Gender feminine.

Type species. Elderra toorlooensis sp. nov. from the Miocene of Australia.

Diagnosis. Sulcate. Beak suberect, beak ridges sharp; symphytium with median and lateral ridges; cardinal margin curved. Hinge platform with hinge trough. Loop without septal connecting bands.

Comments. Elderra contains only one species which is similar in many features to variants of species included in *Magadinella*, but which is notably less variable in size, shape, beak characters, and in the extent of thickening of the cardinalia. Essential distinguishing features are the loop stage and the ridges which demarcate the borders of the symphytium.

Elderra toorlooensis sp. nov.

Fig. 4A–F

Name. From the type locality.

Type material. Holotype NMV P17351 and paratypes NMV P17352, P17353, P86845, P134217–P134220, from the Gippsland Limestone, Bairnsdale Limestone Member (Bairnsdalian, Middle Miocene), Toorloo Creek, Lakes Entrance, Victoria.

Other horizons and localities. Victoria. Gippsland Limestone, Wuk Wuk Marl Member (Batesfordian-Bairnsdalian, Lower–Middle Miocene): lower beds, Skinner's; lower and upper beds, Drier's. Gippsland Limestone, Bairnsdale Limestone Member (Bairnsdalian, Middle Miocene): Pound Swamp; shaft on Rosehill Farm. Tambo River Formation (Mitchellian, Upper Miocene): cliffs on left bank of Tambo River, Swan Reach; cutting near Toorloo Arm. Unknown Tertiary formation: oil shaft dump, Lakes Entrance. All material cited is housed in the Museum of Victoria.

Measurements. (In mm.)

Specimen	Total length	Dorsal valve length	Breadth	Depth
NMV P17351	33.1	29.0	25.9	16.8
NMV P134217	29.8	25.7	22.7	16.3
NMV P134218	31.1	27.2	22.6	15.7
NMV P134219	19.8	26.2	22.5	15.1
NMV P134220	29.5	25.1	21.0	17.7

Description. Outline ovate, biconvex. Anterior commissure gently sulcate. Symphytium slightly concave, with median ridge and lateral ridges at junctions of symphytium and palintropes. Hinge platform trapezoidal in outline; socket ridges projecting posteriorly beyond umbo as two pointed processes, fused anteriorly with swollen crural bases; hinge trough extending length of platform, deeper posteriorly; cardinal process with slightly bulbous anterior surface. Septum short, base thick, crest sharp.

Comments. Little morphological variation is evident in specimens from the environs of Toorloo Creek and the Tambo and Mitchell Rivers. The specimens collected from an oil shaft dump at Lakes Entrance are smaller in size and slightly narrower in outline with stronger curvature of the cardinal margin, features which alone do not justify taxonomic separation.

Adnatida gen. nov.

Name. From the Latin *adnatus* (united), in reference to the components of the cardinalia. Gender feminine.

Type species. Magasella deformis Tate, 1880 from the Eocene of Australia.

Other species. A. gnangarensis sp. nov.

Diagnosis. Sulcate. Beak pointed, erect, foramen small; symphytium concave; beak ridges and cardinal margin curved. Hinge platform heavily thickened without hinge trough or pits, with posterior surface of cardinal process only identifiable structure.
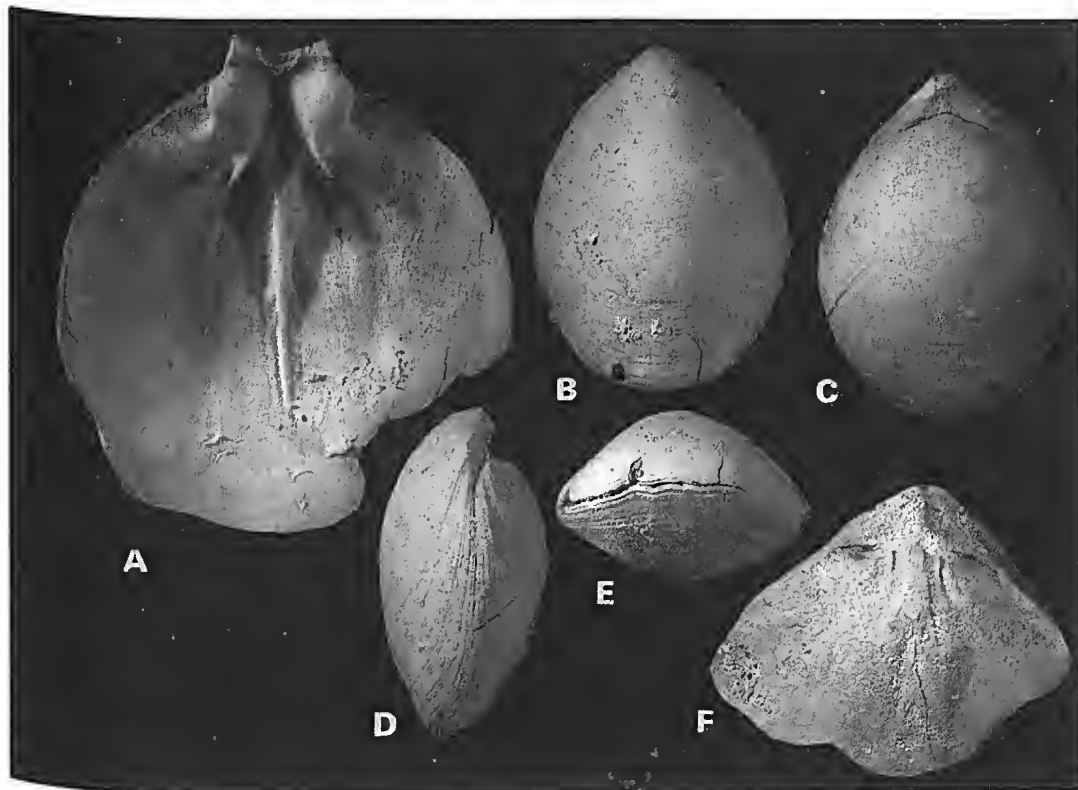
Fig. 4. A–F, *Elderra toorlooensis* sp. nov. A, paratype NMV P17352, dorsal interior, × 2.6. B–E, holotype NMV P17351, dorsal, ventral, lateral and anterior (ventral valve uppermost) views, × 1.25. F, paratype NMV P17353, ventral interior × 1.7.

Comments. The heavily thickened hinge platforms of the two species included in *Adnatida* appear to contain no sites for muscle attachment other than the posterior surface of the cardinal process (attachment surface of the diductor muscles). The absence of a hinge trough or pits, together with the small erect beak and tiny foramen, are indicators of an atrophied pedicle system and a free-lying existence. The appearance of the hinge platform suggests that a lifestyle characteristic of species of *Anakinetica* would have preceded loss of pedicle function in the species of *Adnatida*.

The species of *Adnatida* may be differentiated externally by the curvature of the cardinal margin (moderate in *A. deformis*, strong in *A. gnangarensis*), degree of sulcation (moderate in *A. gnangarensis*, strong in *A. deformis*), shape (broadly ovate in *A. deformis*, pyriform in *A. gnangarensis*) and in the pronounced convexity of the dorsal valve of *A.deformis*. The loop of neither species has been preserved, but the condition of the septum suggests that the loop of *A.*

deformis would show ascending and descending branches, whereas that of *A. gnangarensis* would have fused branches with thin, lateral connecting bands.
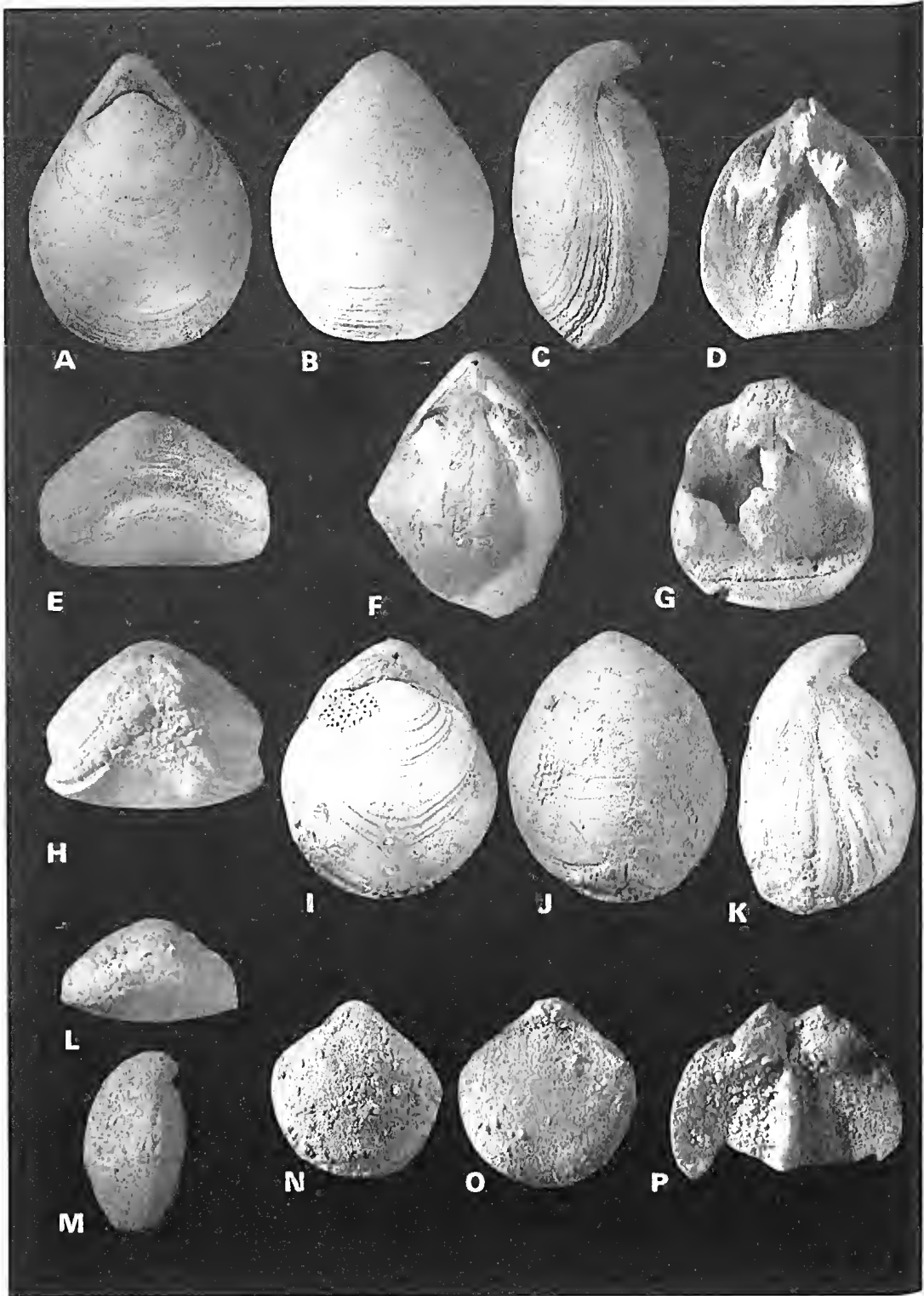
Adnatida deformis (Tate, 1880)

Fig. 5G–K

Magasella deformis Tate 1880: 165–166, pl. 10, fig. 5a–c.
Magadina(?) deformis.—Thomson 1927: 267.

Type material. Five syntypes, SAM T888A–E, from the Tortachilla Limestone (Eocene), Maslin Bay, Aldinga, South Australia.

Description. Length of figured specimen (Fig. 5H–K) 11.7 mm, breadth 9.2 mm, depth 6.6 mm. Strongly sulcate. Outline broadly ovate, greatest width just anterior to mid-length. Symphytium slightly concave; cardinal margin slightly curved. Hinge platform almost circular in outline; posterior surface of cardinal process roughened, slightly lower than surrounding plat-

form. Septum terminating anterior to mid-length, high anteriorly, posterior segment with blunt crest. Loop unknown.

Adnatida gnangarensis sp. nov.

Fig. 5A–F

Name. From the type locality.

Type material. Holotype WAM 90.247 and two paratypes WAM 90.248, 90.249 from the Western Australian Mines Department Bore No. 5, 44.2 to 46.3 m (Pliocene to Lower Pleistocene), Gnangara, Western Australia.

Description. Length of holotype 18.1 mm, breadth 13.4 mm, depth 9.0 mm. Moderately sulcate. Outline pyriform, greatest width just anterior to mid-length. Symphytium concave, cardinal margin strongly curved. Hinge platform outline elongately triangular; cardinal process with lateral segments of posterior surface incurved, rim and presumed anterior surface elevated above surrounding fused elements; anterior border indented at union with septum. Septum terminating anterior to mid-length, crest blade-like. Loop unknown.

Magadina Thomson, 1915

Type species. Magadina browni Thomson, 1915 from the Miocene of New Zealand.

Other species. M. clifdenensis Finlay, 1924; *M. thomsoni* Finlay, 1924; *M. waipariensis* Thomson, 1915; *Magasella lunata* Tate 1899.

Occurrence. Australia, New Zealand; Oligocene–Miocene.

Comments. Thomson's diagnoses (1915, 1927) included Australian species now referred to *Anakinetica* (*compta, cumingii*), *Bouchardiella* (*cretacea*), and *Parakinetica* (*deformis*). The only Australian species now included in the genus is *M. lunata. Magadina* is distinguished from other members of the subfamily in the presence of a deep hinge trough extending the full length of the platform, and in the absence of any medial fusion of the crural bases and/or the anterior surface of the cardinal process.

Magadina lunata (Tate, 1899)

Fig. 5L–P

Magasella lunata Tate 1899: 256, pl. 8, fig. 3, 3a.
(?) *Magadina lunata.*—Thomson 1927: 276.

Type material. Holotype SAM T1724A from Croydon Bore at 122 to 375 m (Miocene), Adelaide, South Australia.

Other horizon and locality. South Australia. Mannum Formation (Lower Miocene): quarry at Mannum. Material housed in the Museum of Victoria.

Measurements. (In mm.)

Specimen	Total length	Dorsal valve length	Breadth	Depth
SAM T1724A	7.1	6.3	6.9	3.8
NMV P134235	6.9	5.7	7.2	4.1
NMV P134236	7.2	6.1	7.0	4.3
NMV P134237	7.1	6.2	6.6	4.3
NMV P134238	5.6	4.8	6.2	2.8

Description. Outline nearly circular; unequally biconvex, dorsal valve nearly plane. Anterior commissure broadly sulcate. Beak suberect, short; deltidial plates conjunct; cardinal margin slightly curved. Hinge platform wide, short; crural bases and socket ridges fused, hinge trough wide, deep; cardinal process small, not projecting into hinge trough. Septum terminating just anterior to mid-length of valve, high anteriorly. Loop with ascending and descending branches separate.

Comments. The Tate Collection in the Department of Geology, University of Adelaide, contains a card with five specimens (T1724A–E) labelled *Magasella lunata*. Only one of these specimens, T1724A, possesses all the external features described and figured by Tate (1899). This specimen is plano-convex with anterior sulcation, a permesothyrid foramen, fused concave deltidial plates, and a curved cardinal margin. The remaining specimens are also plano-convex and sulcate but they display different beak characters (a hypothyrid foramen, rudimentary deltidial plates, and a nearly straight cardinal

←
Fig. 5. A–F, *Adnatida gnangarensis* sp. nov. A–C, E, holotype WAM 90.247, dorsal, ventral, lateral and anterior (dorsal valve uppermost) views, × 2.5. D, paratype WAM 90.248, dorsal interior × 2.5. F, paratype WAM 90.249, ventral interior, × 2.5. G–K, *Adnatida deformis* (Tate, 1880). G, NMV P134212, dorsal interior, × 3.5. H–K, NMV P134240, anterior (ventral valve uppermost), dorsal, ventral and lateral views, × 3.5. L–P, *Magadina lunata* (Tate, 1899). L–O, NMV P134235, anterior (ventral valve uppermost), lateral, ventral and dorsal views, × 4. P, NMV P87579, dorsal interior, × 5.

margin) and were referred to *Malleia portlan-dica* by Richardson (1973b). The above descrip-tion of the species is based on specimens col-lected in the Mannum Formation.

M. lunata is smaller in size than the New Zeal-and species. The largest specimen of *M. lunata* is 7.2 mm in length; the largest specimen of *M. browni* from the Museum of Victoria's col-lection is 13.3 mm. *M. lunata* resembles *M. clif-denensis* in beak and cardinal margin, both of which are shorter than in *M. browni*. The hinge platform of *M. lunata* differs from that of New Zealand species in its greater width and in the socket ridges, which are less strongly convergent and project beyond the margin of the valve for approximately half their lengths.

Pilkena gen. nov.

Name. From the Aboriginal *pilkena* (different). Gender feminine.

Type species. Pilkena compressa sp. nov. from the Olig-ocene of Australia.

Diagnosis. Sulcate. Beak nearly straight, beak ridges sharp; symphytium with low median ridge; cardinal margin slightly curved. Hinge platform with posterior pits for attachment of dorsal adjustor muscles. Loop long, reflected, without septal connecting bands.

Comments. The hinge platform of *Pilkena* is similar to that of *Anakinetica* in the absence of a hinge trough and the presence of posterior pits for attachment of the dorsal adjustor muscles. *Pilkena* is distinguished from *Anakinetica* by the more advanced loop and by the position of the hinge platform relative to the valve surface. The hinge platform of *Pilkena* does not extend be-yond the margin of the dorsal valve, so that the tip of the dorsal umbo is visible. In addition, the posterior surface of the cardinal process is steeply inclined, and consequently both the posterior surface and the posterior pits face pos-teroventrally rather than ventrally as in *Anaki-netica*. These features indicate that substrate relationships would differ in some respect from *Anakinetica*.

Pilkena compressa sp. nov.

Fig. 6A–F

Name. From the Latin *compressus* (compressed).

Type material. Holotype NMV P3629 and paratypes NMV P3627–P3633, P134221 from the Gellibrand Marl (Janjukian, Upper Oligocene), 1.6 km west of Sherbrooke River, near Port Campbell, Victoria.

Additional locality. Jan Juc Formation (Janjukian), Bird Rock Cliffs, Torquay, Victoria.

Measurements. (In mm.)

Specimen	Total length	Dorsal valve length	Breadth	Depth
NMV P3629	27.2	22.4	20.1	9.9
NMV P3627	28.6	24.3	22.6	9.8
NMV P3631	27.3	23.0	20.4	10.3
NMV P3632	25.2	21.8	20.0	9.8
NMV P3628	20.8	18.2	14.9	7.2

Description. Outline ovate, shallowly biconvex, ventral valve carinate, dorsal valve sulcate. Symphytium flat with median ridge. Cardinal platform outline triangular with broad anterior base narrowing to posterior apex; central rounded area (presumed anterior surface of car-dinal process) bordered laterally by socket ridges, posterolaterally by pits and posteriorly by posterior surface of cardinal process. Median septum short, thick, with blade-like ventral edge, without traces of connecting bands. Teeth triangular, base almost flush with edge of valve, walls not excessively thickened.

Aliquantula gen. nov.

Name. From Latin *aliquantulus* (small), in reference to the foramen.

Type species. Waldheimia(?) insolita Tate, 1880 from the Eocene of Australia.

Diagnosis. Weakly sulcate. Beak suberect, fora-men small; beak ridges sharp; cardinal margin curved. Hinge platform with small posterior hinge trough; swollen crural bases fused or almost fused medially; socket ridges not projec-ting beyond umbo; cardinal process small, dis-crete. Loop without septal connecting bands.

Fig. 6. A–F, *Pilkena compressa* sp. nov. A, paratype NMV P3630, dorsal interior, × 2.5. B–D, F, holotype NMV P3629, dorsal, lateral, ventral and anterior (ventral valve uppermost) views, × 1.8. E, paratype NMV P3633, ventral interior, × 1.5. G–L, *Aliquantula insolita* (Tate, 1880). G, NMV P134775, dorsal interior, × 2.3. H, I, K, L, NMV P134774, anterior (ventral valve uppermost), dorsal, lateral and ventral views, × 1.3. J, NMV P134776, ventral interior, × 2.3.
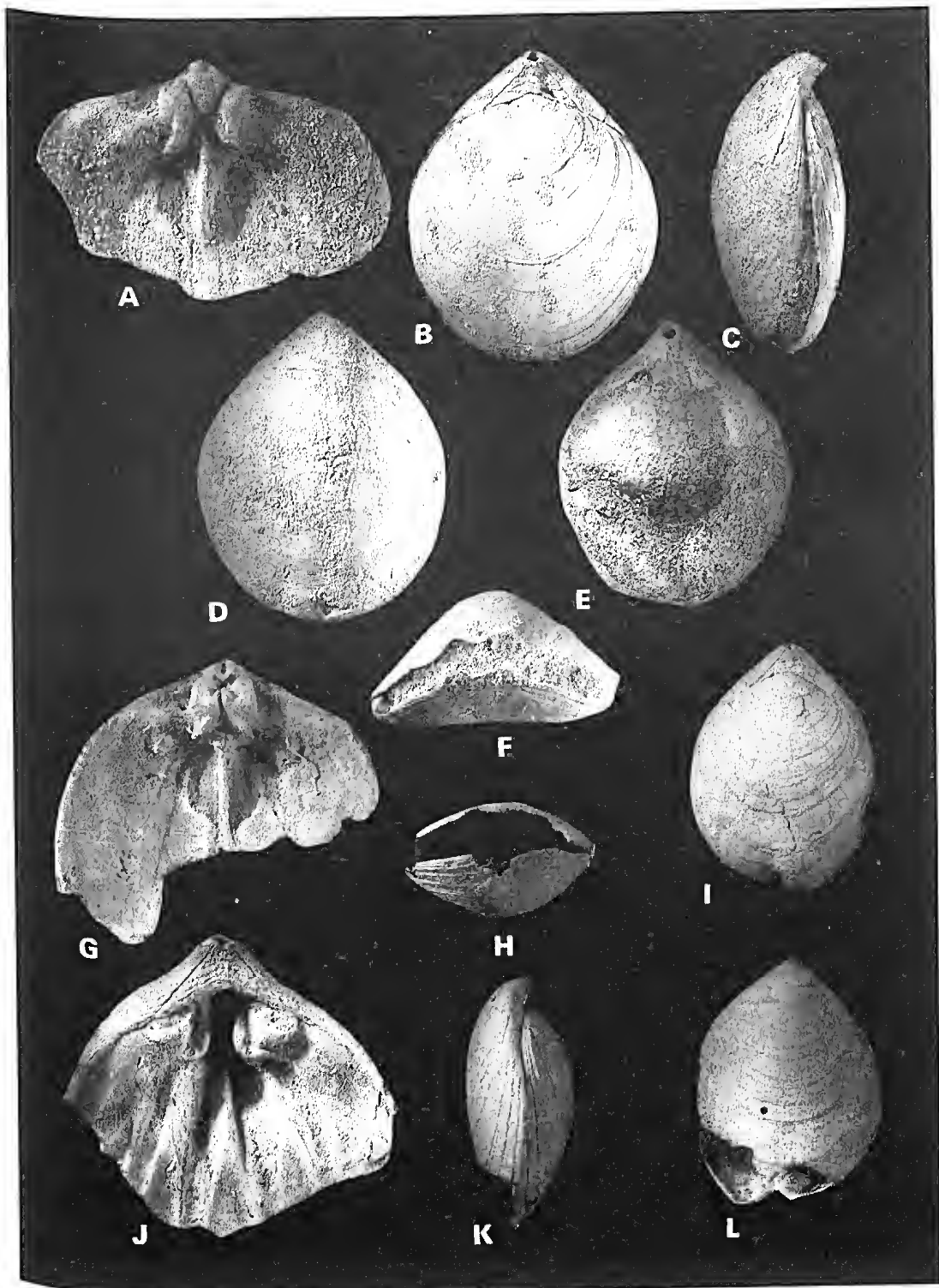
Comments. The partial to total infilling of the hinge trough is one of the characteristic features of members of the Anakineticinae. *Magadinella* and young individuals of *Anakinetica* and *Para-kinetica* show that reduction in size and/or total infilling of the hinge trough is the result of en-largement of the cardinal process (anterior sur-face) which fuses anteriorly with the crural bases. *Aliquantula* shows a different mode of in-filling, with swollen crural bases which may be fused medially but which do not fuse with the cardinal process. As a result, a tiny posterior hinge trough is delimited. In characters of the cardinalia, *Aliquantula* closely resembles the Japanese genus *Nipponithyris*, but the latter dif-fers in beak characters and in loop pattern.

Aliquantula insolita (Tate, 1880)

Fig. 6G–L

Waldheimia(?) insolita Tate 1880: 151–152 (par-tim.), pl. 9, fig. 6b.
Magellania insolita Tate 1899: 282 *(partim.).*
(?) *Stethothyris(?) insolita* Thomson 1927: 282.

Type material. Syntypes SAM T908A–E, G, H, from the Tortachilla Limestone (Eocene), Maslin Bay, Al-dinga, South Australia.

Other horizons and localities. South Australia. Blanche Point Marl (Eocene): Maslin Bay, Aldinga. Victoria. Castle Cove Limestone (Lower Oligocene): Castle Cove (Wilks' locality No.5); mouth of Johanna River. Browns Creek Clay (Eocene): Browns Creek, Aire River district. Browns Creek Clay, greensand member (Eocene): Hamilton Creek, Aire River district. Ma-terial cited is housed in the Museum of Victoria.

Description. Length of figured specimen (Fig. 6 H–I, K–L) 28.8 mm, dorsal valve length, 25.4 mm, breadth 22.1 mm, depth 12.4 mm. Outline ovate, biconvex. Anterior commissure slightly sulcate. Hinge platform outline ovate; socket ridges incurved, not projecting beyond valve margin; crural bases fused with anterior halves of socket ridges; posterior hinge trough small, deep; cardinal process almost circular in outline, anterior surface slightly swollen. Septum short, blade-like, without loop attachments. Ventral valve interior with heavily thickened postero-lateral walls, beak cavity reduced to narrow tun-nel. Hinge teeth irregular in outline, overlying heavy lateral thickenings in posterior region of valve immediately anterior to beak.

Comments. Of Tate's syntypes, specimen SAM T908A has previously been referred to *Aldingia furculifera* by Richardson (1973a).

REFERENCES

CHAPMAN, B. E. & RICHARDSON, J. R., 1981. Recent species of *Neothyris* (Brachiopoda: Terebratel-linae). *New Zealand Journal of Zoology* 8: 157–161.

ETHERIDGE, R., JR, 1876. On some species of *Terebra-tulina, Waldheimia* and *Terebratella* from the Upper Tertiary deposits of Mount Gambier and the Murray River cliffs, South Australia. *Annals and Magazine of Natural History* 17: 15–22.

HATAI, K. M., 1940. Cenozoic Brachiopoda from Japan. *Tohoku University Japan Science Re-ports,* second series (Geology) 20: 1–413.

JOHANSEN, M. B., 1987. Brachiopods from the Maastrichtian–Danian boundary sequence at Nye Klov, Jylland, Denmark. *Fossils and Strata* 20: 1–99.

MACKINNON, D. I., 1987. The influence of Austral-asian–Antarctic plate tectonics and palaeocea-nographic development on the morphology and inferred life habits of New Zealand Neogene brachiopods. *Palaeogeography, Palaeoclimato-logy, Palaeoecology* 48: 63–73.

PRITCHARD, G. B., 1896. A revision of the fossil faunas of the Table Cape beds, Tasmania, with de-scriptions of new species. *Proceedings of the Royal Society of Victoria* 8: 74–150.

RICHARDSON, J. R., 1973a. Studies on Australian Cainozoic brachiopods 2. The family Laquei-dae. *Proceedings of the Royal Society of Victoria* 85: 117–126.

RICHARDSON, J. R., 1973b. Studies on Australian Cainozoic brachiopods 3. The subfamily Bou-chardiinae. *Proceedings of the Royal Society of Victoria* 85: 128–132

RICHARDSON, J. R., 1975. Loop development and the classification of terebratellacean brachiopods. *Palaeontology* 18: 285–314.

RICHARDSON, J. R., 1981a. Brachiopods and pedicles. *Paleobiology* 7: 87–95.

RICHARDSON, J. R., 1981b. Distribution and orien-tation of six articulate brachiopod species from New Zealand. *New Zealand Journal of Zoology* 8: 189–196.

RICHARDSON, J. R., 1987. Brachiopods from carbon-ate sands of the Australian shelf. *Proceedings of the Royal Society of Victoria* 99: 37–50.

STEINICH, G., 1968. Neue Brachiopoden aus der Rugener Schreibkreide (Unter- Maastricht) III. *Dalliglas nobilis* gen. et sp. nov. und *Kingena* sp. *Geologie* 17: 336–347.

STREZLECKI, P. E. DE, 1845. *Physical Description of New South Wales and Van Dieman's Land.* Longman, Brown & Co., London.

TATE, R., 1880. On the Australian Tertiary pallio-branchs. *Transactions of the Royal Society of South Australia* 3: 140–170.

TATE, R., 1899. A revision of the older Tertiary Mollusca, Part 1. *Transactions of the Royal Society of South Australia* 23: 249–277.

TENISON-WOODS, J. E., 1865. The Tertiary rocks of South Australia. Part 3. Brachiopoda. Paper read before the Adelaide Philosophical Society, 5 September 1865, and published in "The Register", a daily newspaper, 3 p.

THOMSON, J. A., 1915. Brachiopod genera: the position of shells with magaselliform loops, and of shells with bouchardiform beak characters. *Transactions of the New Zealand Institute* 47: 392–403.

THOMSON, J. A., 1927. *Brachiopod Morphology and Genera (Recent and Tertiary).* New Zealand Board of Science and Art, Manual No. 7, 338 p.

KYARRANUS MOORE (ANURA, LEPTODACTYLIDAE) FROM THE TERTIARY OF QUEENSLAND

Michael J. Tyler

Department of Zoology, University of Adelaide, Box 498 GPO, Adelaide, South Australia 5001

Tyler, M.J., 1991:06:30. *Kyarranus* Moore (Anura, Leptodactylidae) from the Tertiary of Queensland. *Proceedings of the Royal Society of Victoria* 103 (1): 47–51. ISSN 0035-9211.

The first fossil record of the leptodactylid frog *Kyarranus* Moore is from the Tertiary of northwestern Queensland. Sixteen specimens of the new species *K. borealis* have been recovered and described from a series of Oligo–Miocene sites far to the north of the geographic range of the three extant congeners. Ilial characters provide evidence to sustain the recognition of *Philoria* Parker as a distinct genus.

THE LEPTODACTYLID frog genus *Kyarranus* Moore, 1958 was erected to accommodate the species *K. sphagnicolus* Moore, 1958 from northeastern New South Wales, and *Philoria loveridgei* Parker (1940) from the adjacent portion of southeastern Queensland. A third species subsequently was referred to it, *K. kundagungan* Ingram & Corben, 1975.

Kyarranus is most closely related to the genuinely monotypic *Philoria* Spencer of Mt Baw Baw, Victoria. Each of the *Kyarranus* and *Philoria* species is restricted to localised montane habitats. The breeding biology is specialised. In both genera macrolecithal eggs are laid in moist situations out of water. Larval mouthparts are rudimentary and development is accomplished without feeding (Moore 1961, Littlejohn 1963, Anstis 1981).

Kyarranus has not been reported in the fossil record. However, a series of ilia clearly referable to this genus has been recovered recently from a series of Oligo–Miocene sites at Riversleigh Station in northwestern Queensland. In the present paper the specimens are described as a new species, and the geographic and palaeoclimatic significance of the discovery is discussed.

MATERIAL AND METHODS

The fossil material is deposited in the collections of the Queensland Museum, Brisbane (QM) and the South Australian Museum, Adelaide (SAM). Letters following the abbreviations are departmental identifications.

Comparative studies were based on osteological collections of the Department of Zoology, University of Adelaide. Osteological nomenclature follows Tyler (1976). Methods of measurement and orientation of specimens follows the techniques described by Tyler (1989).

Details of sites, stratigraphy, etc. are provided by Archer et al. (1989).

SYSTEMATICS

Family LEPTODACTYLIDAE Werner, 1896
Subfamily LIMNODYNASTINAE·Lynch, 1971

Genus **Kyarranus** Moore, 1958

The description of the ilial features of the genus by Tyler (1976) was based on *K. sphagnicolus* and *K. kundagungan* (reported there as "*Kyarranus* sp."). Since that date specimens of *K. loveridgei* have become available, and they do not differ conspicuously from the other species (Fig. 1). In all species the dorsal prominence and dorsal protuberance are particularly well-developed, and commonly project anteriorly as a spine. This feature is unique to *Kyarranus*.

Kyarranus borealis sp. nov.

Fig. 2

Holotype. QM F18167, an almost entire left ilium collected at RSO Site, Riversleigh Station, Queensland.

Description of holotype. Ilial shaft cylindrical and very slightly curved; almost entire. Very shallow grooves on medial surface at proximal and distal extremities.

Acetabular fossa very large, deep and with prominent rim bounding inferior half. Dorsal margin of acetabular fossa situated slightly superior to inferior margin of ilial shaft. Preacetabular zone evenly rounded and moderately
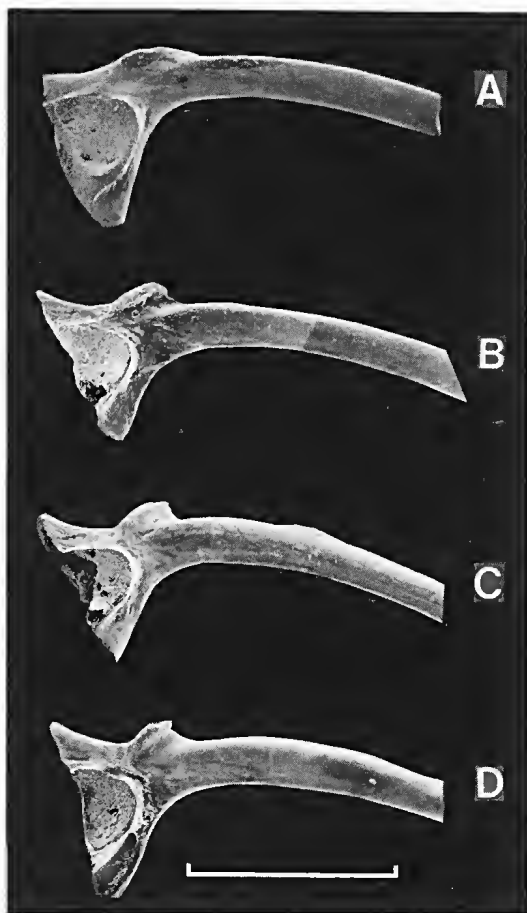
Fig. 1. Comparison of ilia of extant species of *Philoria* and *Kyarranus*. A, *Philoria frosti*; B, *Kyarranus kundagungan*; C, *K. loveridgei*; D, *K. sphagnicolus*. Scale bar = 5 mm.

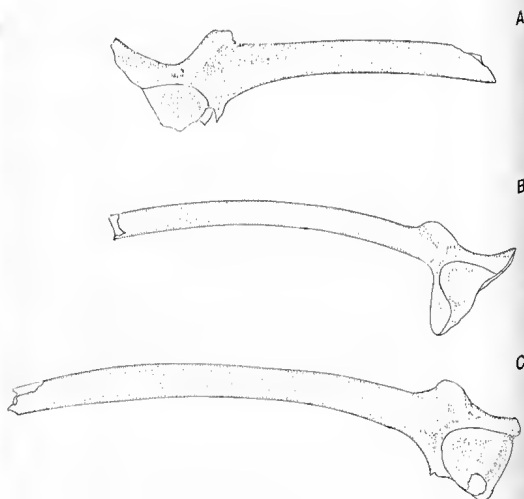Fig. 2. Ilia of *Kyarranus borealis* sp. nov. A, QM F18169 (paratype); B, SAM P31238 (paratype); C, QM F18167 (holotype).

developed. Ventral acetabular expansion (VAE) missing. Dorsal acetabular expansion (DAE) narrow and incomplete. Dorsal prominence well- developed and conspicuous. Dorsal protuberance projecting laterally and extremely conspicuous. Anterior margin of dorsal prominence extends to position located anterior to anterior margin of acetabulum.

Length of ilium 16.1 mm; DAE/VAE cannot be estimated with any degree of confidence.

Paratypes. There are 15 paratypes: Gag Site QM 18160, 18166, SAM P31237; Last Minute Site QM F18163; Neville's Garden Site QM F18169–70, R.S.O. Site QM F18161, 18165; Camel Sputum Site QM F18162, 18168, 18171, SAM P31238; Upper Site SAM P31239; Outasite Site QM F18172; Wayne's Wok Site QM F18164.

Variation. Fourteen of the 15 paratypes have an incomplete shaft. The complete specimen (SAM P31238) measures 8.7 mm compared with 16.1 mm for the holotype. No significance is attributed to this difference beyond ontogenetic; comparable variation in size was noted in *Lechriodus intergerivus* at Riversleigh Station (Tyler 1989) and the projected sizes of many of the incomplete ilia approximate the holotype. The proximal portions of each of the ilia, although commonly lacking entire dorsal or ventral acetabular expansions, conform to the shape of the holotype.

Comparison with other species. It is evident that *K. borealis* may have been a slightly larger species than any of the extant congeners. As determined by plotting the regression line of ilial length upon snout to vent length of extant species (Fig. 3), the holotype of *K. borealis* would have had a snout to vent length of 37.9 ± 0.67 mm. This figure compares with upper limits of 31 mm for *K. loveridgei*, 30 mm for *K. kundagungan* and 37 mm for *K. sphagnicolus*.

Etymology. The adoption of *borealis* (L.) of "northern" refers to the far northern position of the type locality compared with the geographic distributions of extant species.
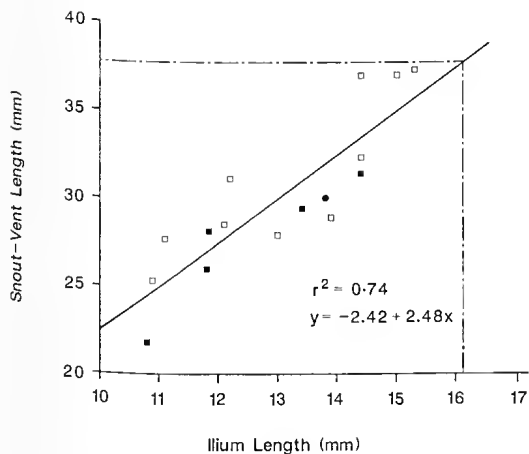
Fig. 3. Length of ilia of *Kyarranus* species plotted against snout to vent length. Assumed snout to vent length of largest specimen of fossil species indicated by broken lines, t- value for slope 6.365, p < 0.001. For x = 16.1, y = 37.9 (95% confidence limits = 36.8-38.2). Closed squares = *K. loveridgei*; open squares = *K. sphagnicolus*; closed circle = *K. kundagungan.*

DISCUSSION

Discovery of *Kyarranus* in the Tertiary of northern Queensland is significant in its contribution to an understanding of the origin and dispersal of Australian frogs and the palaeoenvironmental implications. Extant *Kyarranus* are confined to three isolated montane areas which are variously forested, and where there is a carpet of low growing vegetation and decomposing material within which the frogs live and deposit spawn.

The three extant *Kyarranus* species are allopatric and clustered around the eastern extremity of the Queensland–New South Wales border (Fig. 4). The evident close phylogenetic relationship to *Philoria* that has caused the status of *Kyarranus* to be questioned indicates that a shared ancestral stock once extended through New South Wales and eastern Victoria.

The presence of *K. borealis* in the Tertiary of northwestern Queensland indicates a much more widespread geographic distribution than has been appreciated, and emphasises the relict nature of the extant populations. Extinction in the northwest and intermediate areas can be attributed to the first onset of aridity. However, the existence at the Riversleigh sites raises the question of why this genus did not extend its range farther north into New Guinea when opportunities arose.
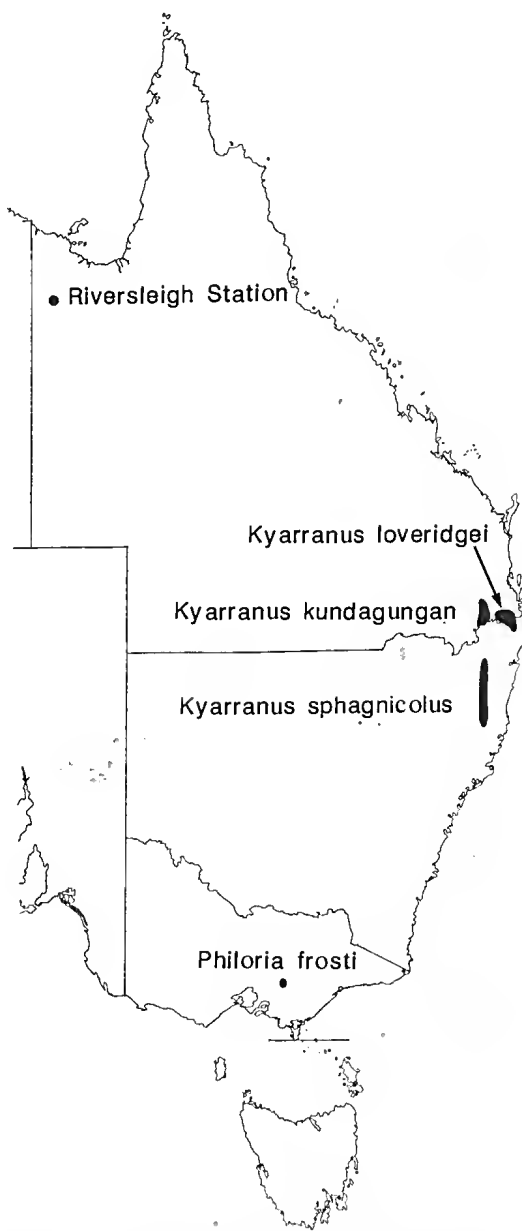

Fig. 4. Geographic distribution of species of *Kyarranus* and *Philoria.* The extent of *K. sphagnicolus* so far south is based on locality records of Webb (1989).

A partial parallel is the distribution of *Lechriodus* Boulenger which is abundant at Riversleigh sites but exhibits a similar gap to the northern limit of the (single) extant species (Tyler 1989, Tyler et al. 1990). However, *Lechriodus* has three extant species in New Guinea.

Conceivably *Kyarranus* does occur in the New Guinea highlands but has yet to be found there. This proposition is plausible when it is noted that the leptodactylid genus *Mixophyes* Günther, with five members well-known from the rainforests of eastern Australia, has only recently been reported from New Guinea (Donellan et al. 1990). If such large and conspicuous frogs escaped attention, the absence of *Kyarranus* in New Guinea may be more apparent than real.

The only area in Australia where the suite of genera reported from Riversleigh (*Lechriodus, Limnodynastes* Fitzinger, *Crinia* Girard, *Litoria* Tschudi and *Kyarranus*) coexist today is along the Queensland–New South Wales border. Three of the genera (*Kyarranus, Lechriodus* and *Limnodynastes*) share the habit of depositing ova in a foam nest. The last two (and *Megistolotis*) create the nest in an identical fashion (Tyler & Davies 1979), but the method in *Kyarranus* (and *Philoria*) has not been observed. Given the complexity of that behavioural activity, concepts of parsimony dictate that the habit evolved in a common ancestor. Elucidation of the Riversleigh frog fauna will clearly lead to an understanding of Oligo–Miocene environments there.

Cogger, Cameron & Cogger (1983) referred *Kyarranus* to the synonymy of the monotypic genus *Philoria* Spencer of Mt Baw Baw in Victoria but did not provide information to substantiate that decision. Accordingly, the synonymy was not accepted by Frost (1985). *Kyarranus* is smaller than *Philoria*, and lacks the hypertrophied dermal glands of that genus. The genera also differ in the arrangement of several skull bones, as pointed out by Lynch (1971). The ilium of *Philoria* differs from that of *Kyarranus* in having a lower dorsal, acetabular expansion, a much less pronounced dorsal prominence and dorsal protuberance, and a reduced pre-acetabular zone (Fig. 1). Given the inherent conservatism of the ilium, the distinctions listed above support the recognition of *Kyarranus* as distinct from *Philoria*.

ACKNOWLEDGEMENTS

REFERENCES

Anstis, M., 1981. Breeding biology and range extension for the New South Wales frog *Kyarranus sphagnicolus* (Anura: Leptodactylidae). *Australian Journal of Herpetology* 1: 1–9.

ARCHER, M., GODTHELP, H., HAND, S. J. & MEGIRIAN, D., 1989. Fossil mammals of Riversleigh, northwestern Queensland: preliminary overview of biostratigraphy, correlation and environmental change. *Australian Zoologist* 25: 29–65.

COGGER, H. G., CAMERON, E. E. & COGGER, H. M., 1983. *Amphibia and Reptilia*. Zoological Catalogue of Australia 1, Australian Government Publishing Service, Canberra.

DONELLAN, S. C., MAHONY, M. J. & DAVIES, M., 1990. A new species of *Mixophyes* (Anura: Leptodactylidae) and first record of the genus in New Guinea. *Herpetologica* 46: 266–274.

FROST, D. R., 1985. *Amphibian Species of the World*. Allen Press & Association of Systematic Collections, Lawrence, Kansas.

INGRAM, G. J. & CORBEN, C. J., 1975. A new species of *Kyarranus* (Anura: Leptodactylidae) from Queensland, Australia. *Memoirs of the Queensland Museum* 17: 335–339.

LITTLEJOHN, M. J., 1963. The breeding biology of the Baw Baw frog *Philoria frosti* Spencer. *Proceedings of the Linnean Society of New South Wales* 88: 273–276.

LYNCH, J. D., 1971. Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. *Miscellaneous Publications of the*

Museum of Natural History, University of Kansas 53: 1–238.

MOORE, J. A., 1958. A new genus and species of leptodactylid frog from Australia. *American Museum Novitates* (1919): 1–7.

MOORE, J. A., 1961. The frogs of eastern New South Wales. *Bulletin of the American Museum of Natural History* 121: 149–386.

PARKER, H. W., 1940. The Australasian frogs of the family Leptodactylidae. *Novitates Zoologicae* 42: 1–106.

TYLER, M. J., 1976. Comparative osteology of the pelvic girdle of Australian frogs and description of a new fossil genus. *Transactions of the Royal Society of South Australia* 100: 3–14.

TYLER, M. J., 1989. A new species of *Lechriodus* (Anura: Leptodactylidae) from the Tertiary of Queensland, with a redefinition of the ilial characteristics of the genus. *Transactions of the Royal Society of South Australia* 113: 15–21.

TYLER, M. J. & DAVIES, M., 1979. Foam nest construction by Australian leptodactylid frogs (Amphibia, Anura, Leptodactylidae). *Journal of Herpetology* 13: 509–510.

TYLER, M. J., HAND, S. J. & WARD, V. J., 1990. Analysis of the frequency of *Lechriodus intergerivus* Tyler (Anura: Leptodactylidae) in Oligo-Miocene local faunas of Riversleigh Station, Queensland. *Proceedings of the Linnean Society of New South Wales* 112: 105–109.

WEBB, G. A., 1989. Notes on the biology and conservation of *Philoria sphagnicolus* (Moore 1958) (Anura: Myobatrachidae). *Herpetofauna* 19: 1–6.

OBITUARY

DR R. R. GARRAN

DR RICHARD GARRAN, a life member of the Royal Society of Victoria, died on 8 April 1991, aged 88 years.

Dick, a son of Sir Robert Garran, took his first degree in science at Trinity College, Melbourne University where, apart from his academic pursuits, he distinguished himself by his rowing prowess. From Melbourne he crossed to Imperial College, London to carry out his postgraduate research. From there, he joined what became the Alkali Division of ICI at Winnington, England, in a select group who were regarded then as the scientific aristocrats of the company.

In the early 1930s, Dick was involved in plans to establish alkali manufacture in Australia, and just before World War 2 came to Osborne in South Australia to take charge of what became a successful operation. There he earned quite a reputation for his hard work and his ability to work remarkably long hours without intermission. He spent his last two or three years with ICI at head office, Melbourne, in charge of personnel.

Dick joined the Royal Society of Victoria in 1954, becoming a member of Council in 1957, and was President in 1961–62. From 1969 to 1983 he acted as Honorary Executive Officer for the Society. In recognition of his services to the Society he was made a Life Member in 1983.

At first encounter, Dick seemed a rather quiet, reserved man. On better acquaintance, he proved to be a very warm-hearted person, a cultured, gentle man in the very highest sense, with a delightful dry sense of humour. He will be missed very much by his friends.

J. D. M.

53

STUDIES ON WESTERN AUSTRALIAN PERMIAN BRACHIOPODS 10. FAUNAS FROM THE WOORAMEL GROUP, CARNARVON BASIN

N. W. ARCHBOLD

Victoria College, Rusden Campus, 662 Blackburn Road, Clayton, Victoria 3168
and Department of Geology, University of Melbourne, Parkville, Victoria 3052

ARCHBOLD, N. W., 1991:12:31. Studies on Western Australian Permian brachiopods 10. Faunas from the Wooramel Group, Carnarvon Basin. *Proceedings of the Royal Society of Victoria* 103 (2): 55–66. ISSN 0035-9211.
    The brachiopod faunas from the One Gum and Billidee Formations of the Wooramel Group are reviewed and described. The new species *Neochonetes (Sommeriella) hockingi* is described and the *Strophalosia jimbaensis* zone is proposed for the faunas described herein. The age of the *Strophalosia jimbaensis* zone is discussed, with an Aktastinian (Early Artinskian) age being preferred.

FOR MANY years there has been considerable debate about the stratigraphical and age significance of the Early Permian marine faunas from the Wooramel Group of the Carnarvon Basin. This study investigates the relatively small collections of variably preserved specimens from the dominantly arenaceous sections of the Wooramel Group sequence. A larger fauna from the Jimba Jimba Calcarenite Member will be documented elsewhere, in view of some confusion over the recognition of this unit in the field (cf. Condon 1967, Hocking et al. 1987).

STRATIGRAPHY

The Permian stratigraphy of the Carnarvon Basin was extensively described by Condon (1967) on the basis of mapping by Bureau of Mineral Resources field parties, and was reviewed and revised by Hocking et al. (1987) on the basis of mapping by Geological Survey of Western Australia field parties. Only the pertinent stratigraphy concerning the Wooramel Group is summarised herein.

The Wooramel Group was defined by Konecki et al. (1958: 28) as the predominantly arenaceous sequence, with few marine fossils, above the surface of the disconformity on top of the Callytharra Formation and conformably below the Byro Group. They divided the Group into three formations (the Nunnery Sandstone, One Gum Formation and Keogh Formation in ascending order) in the type locality region on the Wooramel River, Byro Sub-Basin. The Wooramel Group interval of sediments had previously been recognised by such workers as Condit (1935), Condit et al. (1936), Raggatt (1936), Teichert (1952) and Condon (1954). McWhae et al. (1958) had access to the manu-

script of Konecki et al. (1958) and were the first to cite the names of the formations proposed by Konecki et al.

Other formations in the Wooramel Group were named or described by Condon (1954, 1962a, 1962b, 1965) and in McWhae et al. (1958). Substantial simplification and revisions of the terminology of the Wooramel Group were proposed by van de Graaff et al. (1977) and Hocking et al. (1980). The collections described in the present study come from the One Gum Formation, Byro Sub-Basin (*sensu* Konecki et al. 1958, also Dickins 1956) and the Billidee Formation of the Merlinleigh Sub-Basin (*sensu* Hocking et al. 1987). For convenience, these two stratigraphical names are used in this study.

PREVIOUS FAUNAL STUDIES

Most faunal studies involving the Wooramel Group assemblages have been based on field observations or unpublished palaeontological reports (e.g. see Condon 1962a, 1967, Dickins 1956, Cockbain 1979). On the basis of material observed and collected by Bureau of Mineral Resources field parties during the 1950s, Dickins (1963) was able to demonstrate that the bulk of the Wooramel Group was characterised by "rather unsatisfactory" material that appeared to be "closer to the older Fossil Cliff/ Nura Nura assemblage than to the younger fauna of the Byro Group" (Dickins 1963: 14). This was to characterise Stage C marine faunas of the Western Australian Permian sequences which were "marked by the absence rather than the presence of a marine fauna" (Dickins 1963: 20).

Dickins (1963: 14) also drew attention to the small bivalve and brachiopod fauna in the top-

most beds of the Wooramel Group which is identical with the fauna found in the immediately overlying Byro Group, reflecting "the deepening of the basin and the initial development of more definite off-shore marine conditions in those places". This fauna, found in the top of the Keogh and Billidee Formations, was included in Stage D by Dickins (1963). The occurrence of the ammonoids *Neocrimites* sp. and *Bamyaniceras* sp. in beds high in the Billidee Formation (Cockbain 1980) also links this fauna with the lowest fauna of the Byro Group, generally regarded as being early Baigendzhinian in age.

While there is little disagreement as to the age of the uppermost Wooramel Group faunas, this is not the case for the bulk of the Wooramel Group. Dickins (1963) considered that the close relationship of his Stage C assemblages with those of his Stage B assemblages indicated an age for Stage C of Early Artinskian (Aktastinian). He considered Stage C to be immediately younger than the Sterlitamakian fauna of the underlying Callytharra Formation with, by implication, the disconformity between the two stratigraphical units representing a very minor interval of time.

However, the discovery of a specimen of the ammonoid *Pseudoschistoceras* from beds near the top of the Cordalia Sandstone (a lateral equivalent of the Nunnery Sandstone) resulted in Cockbain (1980) considering the entire Wooramel Group to be of early Baigendzhinian age. *Pseudoschistoceras* is generally considered to indicate a Baigendzhinian age (Glenister et al. 1983) but is only known from three described localities and is listed from the Kungurian by Bogoslovskaya (1988), indicating that it's full stratigraphical range may not be fully understood. Runnegar (1969) and Waterhouse (1970) regarded the recognition of Stage C as unwarranted and so merged it with Stage B. As a result Cockbain (1980: 104) considered that Stage B had a "fairly long time range and occurs at a number of shelly horizons, often of limited extent, and hence cannot be used for detailed biostratigraphical correlation".

AGE OF WOORAMEL GROUP

The fossils figured and described herein include the following:
?*Streptorhynchus* sp.
Permorthotetes sp.
Neochonetes (Sommeriella) hockingi sp. nov.

Strophalosia jimbaensis Archbold, 1986
Aulosteges sp.
Fusispirifer sp.
Neospirifer sp.
?*Cleiothyridina* sp.
?*Aviculopecten* sp.

While the preservation of specimens as natural ferruginous casts and internal and external moulds is of variable quality, the overall affinity of the fauna is closer to that of the Callytharra Formation than to that of the overlying fauna of the Madeline/Coyrie Formation. Nevertheless the Wooramel Group species are distinctive, and of particular importance are species of *Neochonetes (Sommeriella)* and *Strophalosia*. Chonetid brachiopods evolved rapidly during the Permian in Western Australia (e.g. see Archbold 1981) and are invaluable for correlation, while *Strophalosia* species are also important for biostratigraphy (e.g. see Clarke 1990).

A formal zone is proposed herein for Wooramel Group faunas, namely the *Strophalosia jimbaensis* zone, based on a species that is found in both the One Gum and Billidee Formations. The species is also present in the Jimba Jimba Calcarenite where the distinctive species *Globiella flexuosa* (Waterhouse) is also found (Archbold 1983). The Jimba Jimba fauna, currently being investigated by me, appears to be related to that of the Callytharra Formation but is distinct at the species level, adding support to the biostratigraphical recognition of Stage C of Dickins (1963).

In view of the relatively close relationship of many of the Wooramel Group species to those from the Callytharra Formation (see comparisons below), I agree with Dickins (1963) that the disconformity between the two units does not represent a major break in time (perhaps just the late Sterlitamakian). As a result, not withstanding the significance of the occurrence of the ammonoid *Pseudoschistoceras* sp., I prefer an Aktastinian age assignment for the Wooramel Group. Comparison of a few species of the fauna with forms from Sterlitamakian or Aktastinian horizons elsewhere also strengthens the proposed Aktastinian age.

COLLECTIONS AND LOCALITIES

All specimens are registered with the Geological Survey of Western Australia (GSWA F), Perth or with the Commonwealth Palaeontological Collections (CPC) of the Bureau of Mineral Resources, Geology and Geophysics, Canberra.

Specimens were found at the following localities:

Geological Survey of Western Australia locality 94217, from a solitary peak west of Mt Sandiman–Moogooree Road about 12 km north of Mt Sandiman Homestead, Kennedy Range 1:250,000 sheet. Photo reference, Kennedy Range 1968: Run 3, Photo 214, Point 547. From midway up hill where two coquina bands outcrop. Lower band with *Neochonetes (Sommeriella)* and upper (2 m higher) with *Strophalosia*. Billidee Formation.

Bureau of Mineral Resources locality WB 9, 1.25 miles (2 km) on a bearing of 285° from Keogh Hill. Base of One Gum Formation.

Bureau of Mineral Resources locality WB 69, 2.24 miles (3.5 km) on a bearing of 258° from Keogh Hill. Base of One Gum Formation.

Bureau of Mineral Resources locality 7864, 0427, Glenburgh Run 13A, Photo 5009, 2.4 km on a bearing of 276° from Keogh Hill. Base of One Gum Formation.

SYSTEMATIC PALAEONTOLOGY

Phylum BRACHIOPODA
Order STROPHOMENIDA Öpik, 1934
Suborder ORTHOTETIDINA Waagen, 1884
Superfamily ORTHOTETACEA Waagen, 1884
Family STREPTORHYNCHIDAE Stehli, 1954

Genus **Streptorhynchus** King, 1850

Type species. Terebratulites pelargonatus Schlotheim, 1816.

?Streptorhynchus sp.

Fig. 1C

Comments. A single specimen (CPC 24502) of a ferruginous cast of a dorsal valve exterior (specimen 24 mm wide, 26 mm long) may represent the occurrence of *Streptorhynchus* or a related genus in the basal One Gum Formation assemblage (locality BMR 7864, 0427). The specimen
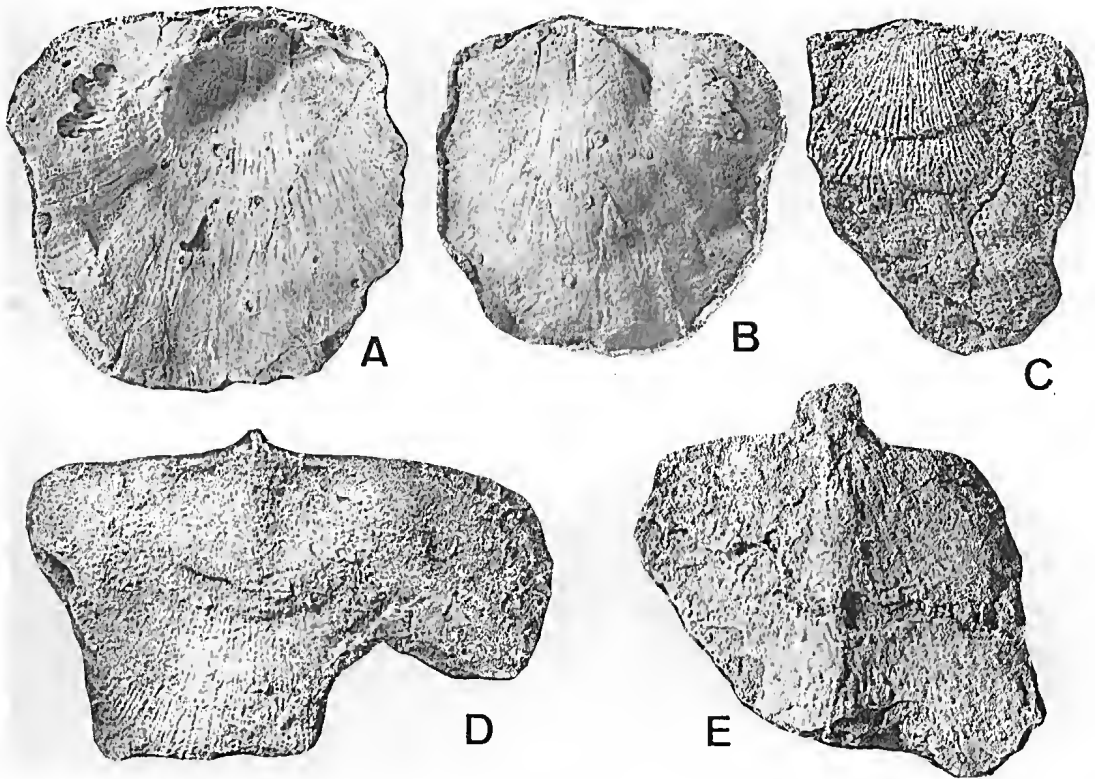

Fig. 1. A, B, D, *Permorthotetes* sp. A, B, CPC 24503, latex cast of incomplete dorsal valve internal mould and the internal mould, × 1.4, × 1.2. D, CPC 24504, natural cast of ventral valve exterior, × 1. C, ?*Streptorhynchus* sp., CPC 24502, natural cast of incomplete dorsal valve, × 1.5. E, *Aulosteges* sp., CPC 24505, natural cast of dorsal valve exterior, × 1.

possesses distinct concentric growth interruptions as in *Arctitreta plicatilis* (Hosking) as described by Thomas (1958), but indicates a larger species than the Callytharra species. Costellae number 8 to 12 per 5 mm and increase predominantly by intercalation although rare bifurcation does occur. Costellae are gently rounded and broaden anteriorly, and hence are not flattened as in *Arctitreta plicatilis* but rather resemble those of *Streptorhynchus crassimurus* Thomas, 1958 from the late Baigendzhinian Noonkanbah Formation, Canning Basin.

Family ORTHOTETIDAE Waagen, 1884
Subfamily ORTHOTETINAE Waagen, 1884

Genus **Permorthotetes** Thomas, 1958

Type species. Permorthotetes callytharrensis Thomas, 1958.

Permorthotetes sp.

Fig. 1A, B, D

Permorthotetes sp.—Thomas 1958: 107.—Condon 1962a: 11.—Condon 1967: 102.
     Orthotetacea nov. gen.—Konecki et al. 1958: 33.

Material. One incomplete mould of a dorsal valve (CPC 24503) from locality BMR 7864, 0427, width 38.5+ mm, length 42+ mm; and one natural cast of a ventral valve exterior (CPC 24504) from locality BMR WB 9, width 67+ mm, length 42 mm.

Comments. Two specimens are consistent with the identification of *Permorthotetes* from the basal One Gum Formation. The dorsal valve internal mould reveals an uneven convex profile and a low median ridge bisecting the muscle field. The cardinal process is unknown. The ventral valve external ferruginous cast is large, wrinkled, irregularly gently convex posteriorly and flat anteriorly. Costellae are fine (about 7 to 8 per 5 mm at 30 to 40 mm from umbo) and increase by intercalation. Intercostal troughs are

wider than costellae. A comparison with *Permorthotetes callytharrensis* Thomas, 1958 is suggested but better material is required for detailed comparisons.

Order CHONETIDA Nalivkin, 1979
Suborder CHONETIDINA Muir-Wood, 1955
Superfamily CHONETACEA Bronn, 1862
Family RUGOSOCHONETIDAE Muir-Wood, 1962
Subfamily RUGOSOCHONETINAE Muir-Wood, 1962

Genus **Neochonetes** Muir-Wood, 1962
Subgenus **Neochonetes** (**Sommeriella**) Archbold, 1982

Type species. Chonetes prattii Davidson, 1859.

Comments. The subgeneric name *Sommeria* Archbold, 1981 was replaced by the name *Sommeriella* by Archbold, 1982. The recognition of subgenera within the large and widely understood genus *Neochonetes* was discussed by Archbold (1981).

### Neochonetes **hockingi** sp. nov.

Fig. 2A–R

Etymology. Named for geologist Roger M. Hocking, discoverer of the chonetid band which yielded the species.

Holotype. GSWA F11247, a natural ferruginous cast of a ventral valve exterior showing the external ornament, from GSWA locality 94217, Billidee Formation, collected by Dr S. K. Skwarko, Geological Survey of Western Australia.

Paratypes. GSWA F43818–F43820, two natural casts of dorsal valve exteriors and one external mould of a dorsal valve; GSWA F43821, F43822, two natural casts of shells; GSWA F43823–F43826, four natural casts of ventral valve interiors; GSWA F43827, F43828, two natural casts of ventral valve exteriors; and GSWA F43829–F43834, five natural casts of dorsal valve interiors and one natural internal mould of a

Fig. 2. Neochonetes (Sommeriella) hockingi sp. nov. A, GSWA F43818, natural cast of dorsal valve exterior, × 3.5. B, GSWA F43819, latex cast of dorsal valve exterior, × 3.5. C, GSWA F43820, natural cast of dorsal valve exterior, × 3.5. D, GSWA F43821, natural cast of shell in dorsal view, × 3.5. E, GSWA F43823, natural cast of ventral valve interior, × 3.5. F, GSWA F43822, natural cast of shell in dorsal view, × 3.5. G, GSWA F43824, natural cast of ventral valve interior, × 3.5. H, GSWA F43825, natural cast ventral valve interior, × 3.5. 1, GSWA F43826, natural cast of ventral valve interior, × 3.5. J, GSWA F11247, holotype, natural cast of ventral valve exterior, × 3.5. K, GSWA F43827, natural cast of ventral valve exterior, × 3.5. L, GSWA F43828, natural cast of worn ventral valve exterior, × 3.5. M, GSWA F43829, natural cast of dorsal valve interior, × 3.5. N, GSWA F43830, natural cast of juvenile dorsal valve interior, × 3.5. O, GSWA F43831, natural cast of juvenile dorsal valve interior, × 3.5. P, GSWA F43832, latex cast of dorsal valve internal mould, × 3.5. Q, GSWA F43833, natural cast of dorsal valve interior, × 3.5. R, GSWA F43834, natural cast of dorsal valve interior, × 3.5.
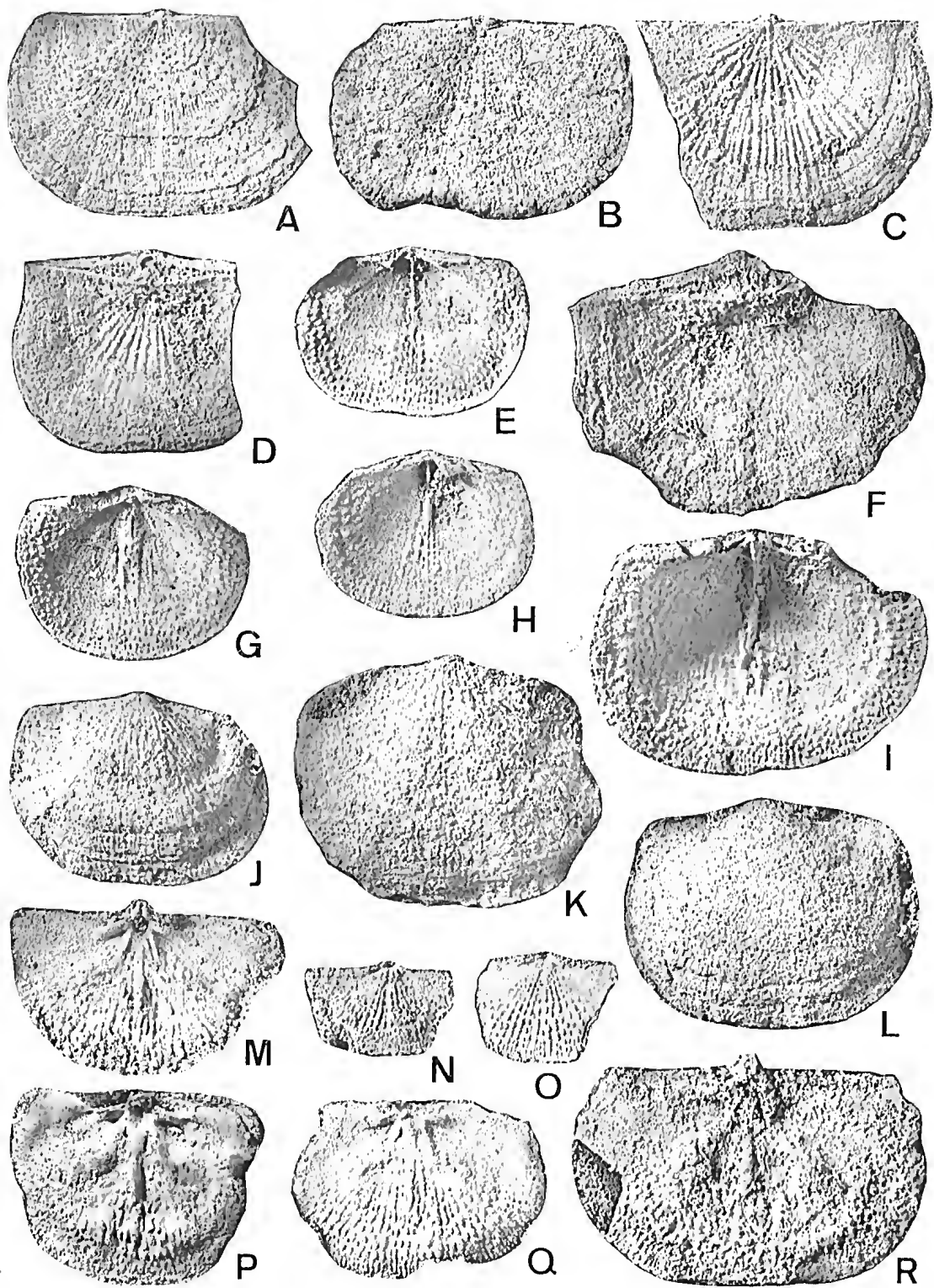
dorsal valve; same locality and collector as holotype.

Size ranges. Maximum width 5.7–14.9 mm; hinge width 5.5–14.2 mm; ventral length 6.5–10.6 mm; dorsal length 4.3–9.3 mm.

Diagnosis. Small *Neochonetes (Sommeriella).* Ventral sulcus weakly developed; dorsal fold low but distinct. External ornament of fine capillae, on average numbering 3 per mm at 6 mm from umbones.

Description. Length of shell just over two-thirds of maximum width. Maximum width just anterior of shell mid-length; hinge width less than maximum width. Ventral valve evenly convex. Sulcus low, broadening anteriorly, arising close to umbo. Dorsal valve gently concave with low median fold often poorly developed. Interareas low, chilidium and pseudodeltidium poorly known. Ornament of capillae increasing by bifurcation and intercalation. Growth lines fine, more pronounced anteriorly.

Casts of worn ventral valves show external ornament poorly; those of worn dorsal valves show progressive absence of growth lines and presence of fine pseudocapillate ornament (5–6 per mm at 6 mm from umbo) reflecting internal subsurface shell structure. Ventral hinge spines poorly known, appear to project at 40° to 45°.

Ventral interior with distinct median septum, over half valve length at maturity, arising under ventral umbo. Parallel vascular trunks usually distinct adjacent to septum. Adductor scars indistinct; diductors large, prominent, gently striated. Remainder of valve floor papillose. Teeth small, sharp.

Cardinal process internally bilobate, externally poorly known. Dorsal median septum distinct, up to 0.6 times valve length. Ontogeny of dorsal septum reveals absence in juveniles, presence well to the anterior of alveolus in submaturity but fused with lateral septa and anterior of alveolus at maturity. Sockets distinct

with pronounced inner socket ridges. Brachial ridges raised and papillose at maturity. Radiating rows of papillae in anterior of dorsal valve.

Discussion. Neochonetes (Sommeriella) hockingi is distinguished from most other Western Australian representatives of the subgenus by its distinctive small size and low ventral sulcus. *N. (S.) robustus* Archbold, 1981 from the early Baigendzhinian Madeline Formation, Carnarvon Basin, is a slightly larger species with a distinctive rounded outline and is more concavo-convex than *N. (S.) hockingi.* The sulcus of *N. (S.) robustus* is virtually absent. The new species shares features with *N. (S.) arabicus* (Hudson & Sudbury, 1959) from the Sterlitamakian to Aktastinian or younger Lusaba Limestone of Oman, an even smaller species with similar dorsal exterior and interior to those of *N. (S.) hockingi.* The Oman species is the smallest representative of *Neochonetes (Sommeriella)* known at present (Archbold & Burrett 1990).

Order PRODUCTIDA Sarycheva & Sokolskaya, 1959
Suborder STROPHALOSIIDINA Waterhouse, 1975
Superfamily STROPHALOSIACEA Schuchert, 1913
Family STROPHALOSIIDAE Schuchert, 1913
Subfamily STROPHALOSIINAE Schuchert, 1913

Genus Strophalosia King, 1844

Type species. Strophalosia gerardi King, 1846.

Strophalosia jimbaensis Archbold, 1986
Fig. 3A–P

Strophalosia nov. sp.—Konecki et al. 1958: 33.
Strophalosia sp.—Condon 1963a: 11.—Condon 1967: 114.—McGann 1976: 47.

Fig. 3. A–P, *Strophalosia jimbaensis* Archbold. A, GSWA F43835, natural cast of dorsal exterior, × 1.3. B, GSWA F43836, natural cast of dorsal valve exterior, × 1.3. C, GSWA F43837, latex cast of ventral valve external mould, × 1.3. D, GSWA F43838, latex cast of ventral valve external mould, × 1.3. E, GSWA F43839, latex cast of ventral valve external mould, × 1.3. F, GSWA F43840, latex cast of ventral valve external mould, × 1.3. G, GSWA F43841, latex cast of ventral valve external mould, × 1.3. H, GSWA F43842, internal mould of ventral valve, × 1.3. I, GSWA F43844, latex cast of dorsal valve internal mould, × 1.3. J, GSWA F43843, latex mould from natural cast of dorsal valve interior, × 1.3. K, GSWA F43845, latex cast of dorsal valve internal mould, × 1.3. L, GSWA F43846, latex cast of dorsal valve internal mould, × 1.3. M, GSWA F43847, latex cast of dorsal valve internal mould, × 1.3. N, GSWA F43848, latex cast of dorsal valve internal mould, × 1.3. O, GSWA F43849, latex cast of dorsal valve internal mould, × 1.3. P, GSWA F43850, latex cast of dorsal valve internal mould, × 1.3. Q, R?, *Aviculopecten* sp., GSWA F43852, F43853, two small specimens, both incomplete, × 1. S, *Fusispirifer* sp., GSWA F43851, incomplete internal mould of ventral valve, × 1.
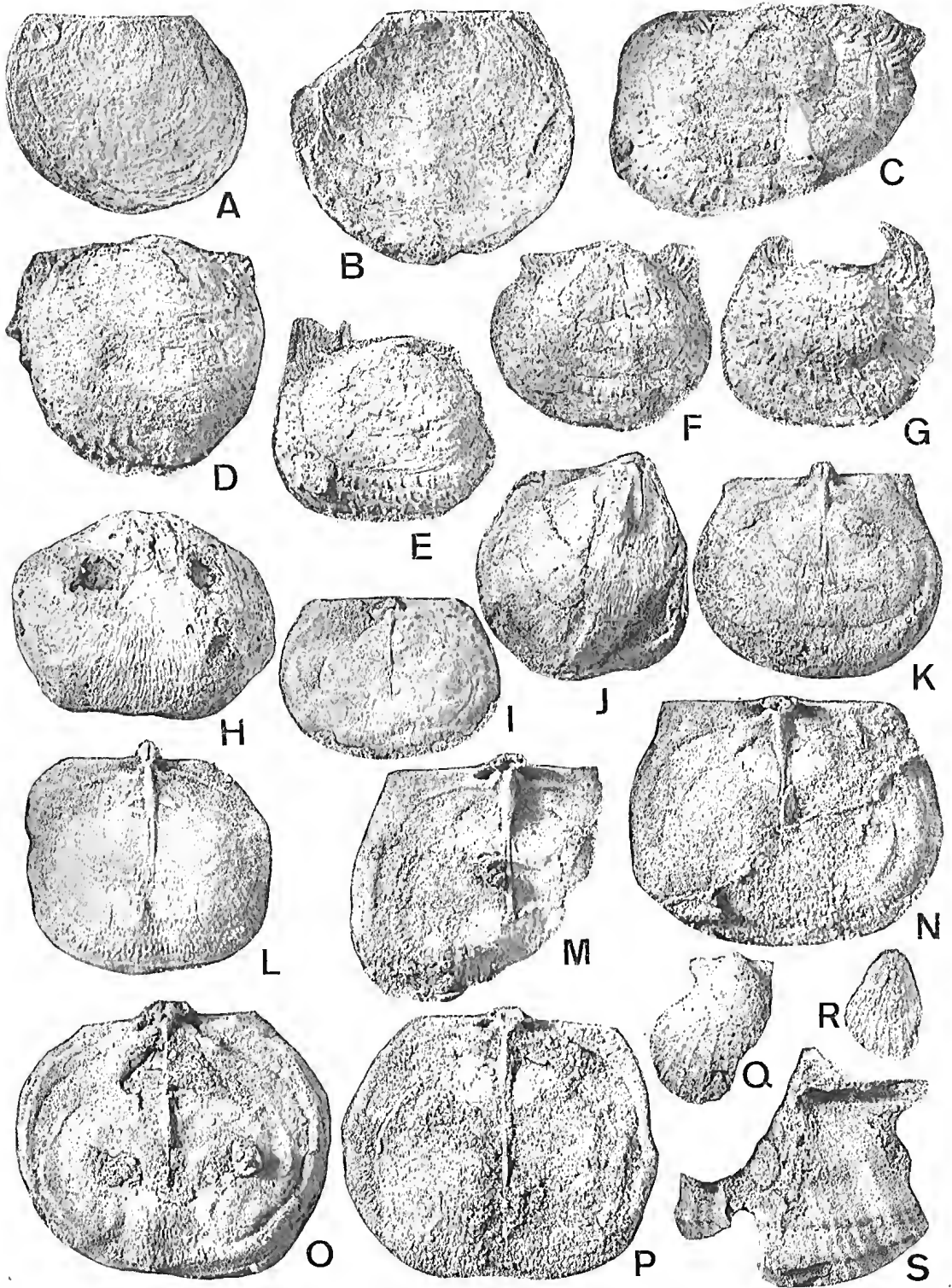
Strophalosia jimbaensis Archbold 1986: 102–104, fig. 2A–G.
   Strophalosia sp. cf. *S. jimbaensis.*—Archbold 1986: 104, fig. 2H–O.

Material. GSWA F43835–43850, two natural ferruginous casts of dorsal valve exteriors, five external moulds of ventral valves, one internal mould of a ventral valve, one natural cast of a ventral valve interior and seven internal moulds of dorsal valves, all from GSWA locality 94217, Billidee Formation, collected by Dr S. K. Skwarko, Geological Survey of Western Australia.

Size ranges. Maximum width 25.4–40.2 mm; hinge width 19.2–28.2 mm; ventral length 20.6–29.4 mm; dorsal length 19.6–32.6 mm.

Diagnosis. Medium to large sized *Strophalosia* with moderately convex ventral valve and concave dorsal valve. Dorsal valve with well defined dimples, growth lamellae and radial capillae, no spines. Ventral valve with hinge spines, two rows on ears, numerous scattered suberect body spines and a shallow median sulcus or flattening.

Comments. Dickins (in Konecki et al. 1958: 33) was the first to recognise "*Strophalosia* nov. sp., resembling a species from the Callytharra Formation" in the basal One Gum Formation assemblage. Eight specimens from the assemblage were figured by Archbold (1986, fig. 2H–O) who compared them with the Jimba Jimba Calcarenite species *Strophalosia jimbaensis*. Different styles of preservation between the type specimens of *S. jimbaensis* and the One Gum specimens prevented unequivocal assignment of the latter to *S. jimbaensis*.
   The well preserved new suite of specimens from the Billidee Formation serves to unite the two collections discussed above and provides additional information on details of the ventral exterior spines and the dorsal interior and cardinal process. Spines on the ventral ears are in two rows and curve back towards the umbo; they are in excess of 8.5 mm in length. Body spines are in rough concentric rows and project laterally and anteriorly near the exterior perimeter of the ventral valve. The dorsal interior possesses a thin median septum about half the valve length at submaturity, but at maturity a thickened median septum is some two-thirds the valve length. Large brachial ridges become prominent at full maturity. The cardinal process is relatively small, bilobed internally and spikelike at submaturity when it projects posteriorly beyond the hinge line of the dorsal valve. At maturity, the cardinal process is broader and more massive, approaches a quadrilobed state internally and projects internally in the plane of the dorsal interarea.
   Several other species of *Strophalosia* have been described since the erection of *S. jimbaensis* by Archbold (1986). *Strophalosia perfecta* Waterhouse & Rao (1989) from the Early Permian of the Bap Formation, Rajasthan is a much smaller species than *S. jimbaensis*, suggesting comparison with the Western Australian Sterlitamakian species *S. irwinensis* Coleman (see Archbold 1986). *S. concentrica* Clarke, 1990 from the Early Permian of Tasmania is a distinct small to medium sized globose species that does not warrant close comparison with *S. jimbaensis*. *S? vollosovitschi* (Fredericks, 1931) as recorded by Abramov & Grigor'eva (1988: 104, pl. 1, figs 23–25, pl. 2, figs 1, 2, 7) from Verkhoyan'ya, northeast Siberia is a large species apparently lacking distinct dorsal external dimples.
   Strophalosia is a characteristic genus of the Early Permian (Asselian–Sakmarian) of Australia (Archbold 1986, Clarke 1990) although ranging younger in Western Australia with the species *S. jimbaensis*. The genus is unknown in the well known Baigendzhinian faunas of the Carnarvon and Canning Basins, although a very rare species (2 specimens?) is known from the early Baigendzhinian fauna of the Mingenew Formation of the Perth Basin (Archbold 1988). The Mingenew species possesses distinctive smaller dorsal exterior dimples than those of *S. jimbaensis*.

Superfamily AULOSTEGACEA Muir-Wood & Cooper, 1960
Family AULOSTEGIDAE Muir-Wood & Cooper, 1960
Subfamily AULOSTEGINAE Muir-Wood & Cooper, 1960

Genus Aulosteges von Helmersen, 1847

Type species. Orthis wangenheimi de Verneuil, 1845 (= *Aulosteges variabilis* von Helmersen, 1847).

Aulosteges sp.

Fig. 1E

Comments. A single natural cast of the exterior of a dorsal valve (CPC 24505) from BMR locality WB 9, basal One Gum Formation, indicates the presence of *Aulosteges* s.l. in the assemblage, on the basis of its distinct, low dorsal median

fold. The specimen shows distinct dimples and a few spine bases but is inadequate for detailed comparison with other Western Australian species described by Coleman (1957).

Order Spiriferida Waagen, 1883
Suborder Spiriferidina Waagen, 1883
Superfamily Spiriferacea King, 1846
Family Spiriferidae King, 1846
Subfamily Neospiriferinae Waterhouse, 1968

Genus **Fusispirifer** Waterhouse, 1966

Type species. Spirifer nitiensis Diener, 1897.

Comments. Fusispirifer was reviewed by Archbold & Thomas (1987) who discussed the subfamilial placing of the genus and its palaeogeographical distribution. An additional species of *Fusispirifer* from the Western Australian Permian was described by Archbold & Skwarko (1988).

Fusispirifer sp.

Fig. 3S, 4A–G, L.

Material. CPC 19894–19897, three ventral valve internal moulds and one external mould of a ventral valve from BMR locality WB 69, basal One Gum Formation. CPC 24506–24509, two natural casts of juvenile ventral valve interiors and two incomplete external moulds of ventral valves from BMR locality 7864 0427, basal One Gum Formation. GSWA F43851 (formerly F11060/1), incomplete internal mould of a ventral valve from GSWA locality 94217, Billidee Formation.

Comments. Fusispirifer is abundant in the Permian of Western Australia (Archbold & Thomas 1987) and the present material indicates the presence of the genus in the Wooramel assemblages. The species is characterised by coarse costae and lateral plications that are variable but usually well developed on juvenile specimens but are poorly developed on the flanks of mature specimens. The Callytharra Formation species *F. carnarvonensis* possesses lower and usually finer ventral valve costae and very subdued lateral flank plications when compared with the material to hand. The younger *F. byroensis* (Glauert) (see Archbold & Thomas 1987) is a distinct flattish species readily distinguished from the Wooramel Group species.

A distinctive internal feature of the Wooramel species is the large, relatively wide ventral muscle field recalling that of the large species *F. wandageensis* from the late Early Permian Wandagee Formation. The Wooramel specimens are closest to *F. carnarvonensis* from the Callytharra Formation but are distinct from that species and with the collection of additional material, particularly dorsal valves, will require the recognition of a new species.

Genus **Neospirifer** Fredericks, 1924

Type species. Spirifer fasciger von Keyserling, 1846.

Neospirifer sp.

Fig. 4H–J

Neospirifer sp.—Konecki et al. 1958: 33.—Condon 1962a: 11.—Condon 1967: 114.—McGann 1976: 51.
Neospirifer sp. B.—Archbold & Thomas 1986: 150, fig. 14 B, C.

Material. One natural cast of a ventral valve interior and one incomplete external mould of a ventral valve (CPC 19898–19899) from BMR locality 7864 0427, and one incomplete external mould of a ventral valve (CPC 24362) from BMR locality WB 69; all from the basal One Gum Formation.

Comments. As noted by Archbold & Thomas (1986: 150), the Wooramel *Neospirifer* species is related to the Western Australian *N. hardmani–N. plicatus* group of *Neospirifer* and appears to represent an intermediate species between the Callytharra and Madeline Formation species. The new material includes a fragment of a mature ventral valve (CPC 19899) which recalls specimens of an undescribed species of *Neospirifer* from the Aktastinian High Cliff Sandstone of the Perth Basin.

Order Athyridida Dagys, 1974
Suborder Athyrididina Boucot, Johnson & Staton, 1964
Superfamily Athyridacea M'Coy, 1844
Family Athyrididae M'Coy, 1844
Subfamily Athyridinae M'Coy, 1844

Genus **Cleiothyridina** Buckman, 1906

Type species. Atrypa pectinifera Sowerby, 1840.
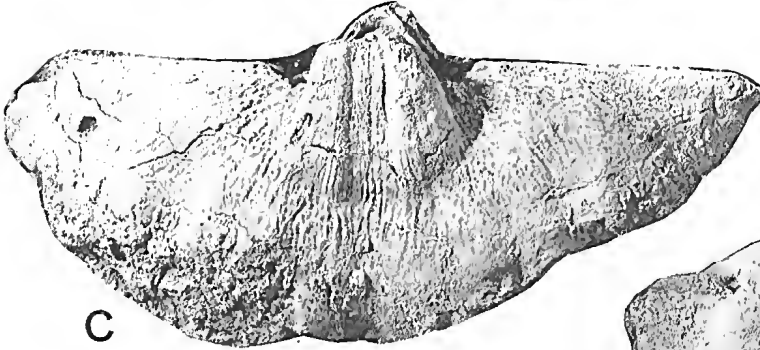
?Cleiothyridina sp.

Fig. 4K

Comments. A single specimen (CPC 24510) of an incomplete natural cast of a juvenile ventral valve interior from BMR locality 7864 0427 may represent an athyrid such as *Cleiothyridina*, judging from what appear to be traces of vascu-
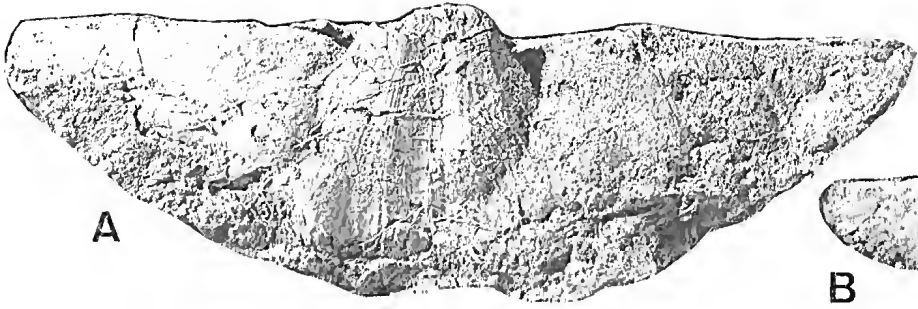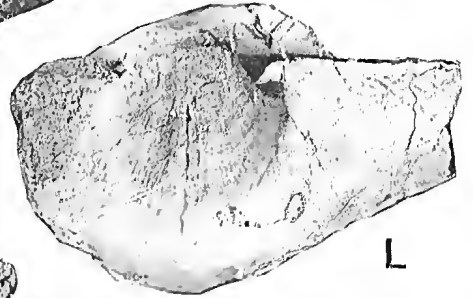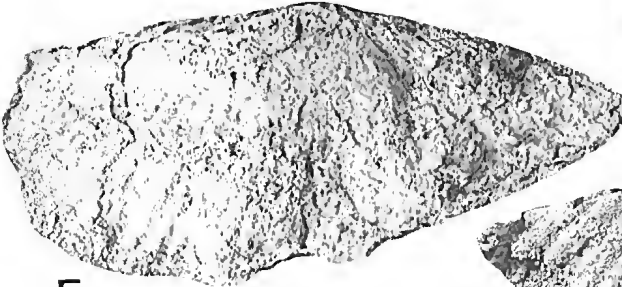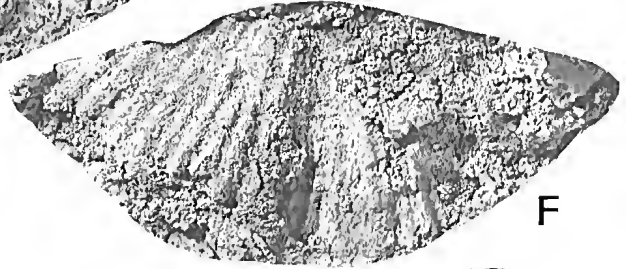
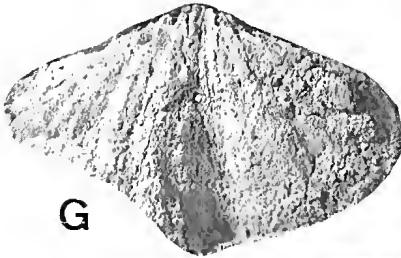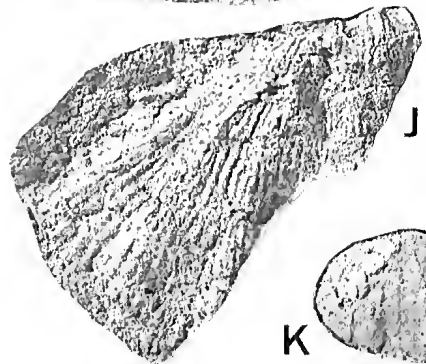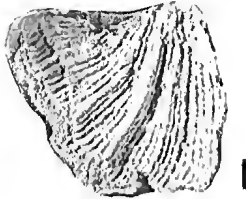*Fig. 4.* A–G, L, *Fusispirifer* sp. A, CPC 19894, internal mould of ventral valve, × 1. B, CPC 24506, latex cast of natural cast of juvenile ventral valve interior, × 1.5. D, CPC 24507, latex cast of natural cast of juvenile ventral valve interior, × 1.5. C, CPC 19895, internal mould of ventral valve, × 1. E, CPC 19896, latex cast of ventral valve external mould, × 1. F, CPC 24508, latex cast of ventral valve external mould, × 1. G, CPC 24509, latex cast of ventral valve external mould, × 1; note that lateral valve extremities are not preserved. L, CPC 19897, internal mould of ventral valve, × 1. H–J, *Neospirifer* sp. H, CPC 19898, latex cast of natural cast of juvenile ventral valve interior, × 1.5. I, CPC 24362, latex cast of ventral valve external mould, × 1. J, CPC 19899, latex cast of incomplete ventral valve external mould, × 1.2. K, ?*Cleiothyridina* sp., latex cast of natural cast of ?juvenile ventral valve interior, × 1.5.

lar impressions. The specimen is inadequate for detailed comment.

Phylum MOLLUSCA
Class BIVALVIA

Comments. For completeness, two small fragmentary specimens (GSWA F43852–43853) from GSWA locality 94217 are figured (Fig. 3Q–R). Judging from descriptions and illustrations of Western Australian Permian Bivalvia provided by Diekins (1963), both specimens probably represent pectinaceans referrable to *Aviculopecten, Etheripecten* or a closely related genus and appear close to forms from the Callytharra Formation.

REFERENCES

References are supplementary to those in Parts 1–9 (*Proceedings of the Royal Society of Victoria*, vol. 91: 181; vol. 93: 109; vol. 95: 237; vol. 96: 83; vol. 97: 19; vol. 98: 97; vol. 99: 19; vol. 100: 21; vol. 102: 1).

ABRAMOV, B. S. & GRIGOR'EVA, A. D., 1988. *Biostratigrafiya i Brakhiopody Permi Verkhoyan'ya.* Nauka, Moscow, 208 p.

ARCHBOLD, N. W., 1988. Permian brachiopod faunas of the Perth Basin, Western Australia – A study of progressive isolation. Ninth Australian Geological Convention, Geological Society of Australia Abstracts, Number 21: 46–47.

ARCHBOLD, N. W. & BURRETT, C. F., 1990. Reassessment of the Arabian Permian chonetid brachiopod *Chonetes arabicus* Hudson & Sudbury. *Proceedings of the Royal Society of Victoria* 102: 121–122.

ARCHBOLD, N. W. & SKWARKO, S. K., 1988. Brachiopods and bivalves of Kungurian (late Early Permian) age from the top of the Coolkilya Sandstone, Carnarvon Basin, Western Australia. *Geological Survey of Western Australia Report* 23: 1–15.

ARCHBOLD, N. W. & THOMAS, G. A., 1987. *Fusispirifer* (Spiriferidae, Brachiopoda) from the Permian of Australia and Afghanistan. *Alcheringa* 11: 175–203.

BOGOSLOVSKAYA, M. F., 1988. O verkhne granitse nizhnego otdela Permskoi sistemy po materialam ammonoidei. In *Permskaya Sistema: Voprosy stratigrafii i razvitiya organischeskogo mira.* Izdatel'stvo Kazanskogo Universiteta, 16–26.

CLARKE, M. J., 1990. Late Palaeozoic (Tamarian: Late Carboniferous–Early Permian) cold-water brachiopods from Tasmania. *Alcheringa* 14: 53–76.

COCKBAIN, A. E., 1979. New Permian samples from the Carnarvon Basin. Geological Survey of Western Australia Palaeontological Report No. 22/1979, 3 p. (unpublished).

CONDIT, D. D., 1935. Oil possibilities in the North West district, Western Australia. *Economic Geology* 30: 860–878.

CONDIT, D. D., RAGGATT, H. G. & RUDD, E. A., 1936. Geology of Northwest Basin, Western Australia. *Bulletin of the American Association of Petroleum Geologists* 20: 1028–1070.

CONDON, M.A ., 1954. Progress report on the stratigraphy and structure of the Carnarvon Basin, Western Australia. *Bureau of Mineral Resources, Geology and Geophysics Report* 15: 1–163.

CONDON, M. A., 1962a. 1:250,000 Geological Series Explanatory Notes. Glenburgh, WA. Sheet G/50-6, Australian National Grid. Bureau of Mineral Resources, Geology and Geophysics, Canberra, 22 p.

CONDON, M. A., 1962b. 1:250,000 Geological Series Explanatory Notes. Kennedy Range, WA. Sheet G/50-1, Australian National Grid. Bureau of Mineral Resources, Geology and Geophysics, Canberra, 28 p.

CONDON, M. A., 1962b. 1:250,000 Geological Series Explanatory Notes. Wooramel, WA. Sheet SG/50-5, International Index. Bureau of Mineral Resources, Geology and Geophysics, Canberra, 20 p.

DICKINS, J. M., 1956. The Permian marine macro-fossils of the Wooramel and Byro Groups of the Wooramel River area, Western Australia. Bureau of Mineral Resources, Geology and Geophysics Record 1956/113, 21 p. (unpublished).

DIENER, C., 1897. The Permian fossils of the Productus Shales of Kumaon and Gurhwal. Memoirs of the Geological Survey of India, Palaeontologia Indica Series 15, 1 (4): 1–54.

GLENISTER, B. F., GLENISTER, L. M. & SKWARKO, S. K., 1983. Lower Permian cephalopods from western Irian Jaya, Indonesia. Geological Research and Development Centre, Palaeontology Series 4: 74–85.

HOCKING, R. M., MOORE, P. S. & MOORS, H. T., 1980. Modified stratigraphic nomenclature and concepts in the Palaeozoic sequence of the Carnarvon Basin. Geological Survey of Western Australia Annual Report (1979): 51–55.

HOCKING, R. M., MOORS, H. T. & VAN DE GRAAFF, W. J. E., 1987. Geology of the Carnarvon Basin Western Australia. Geological Survey of Western Australia Bulletin 133: 1–289.

KONECKI, M. C., DICKINS, J. M. & QUINLAN, T., 1958. The geology of the coastal area between the Lower Gascoyne and Murchison Rivers, Western Australia. Bureau of Mineral Resources, Geology and Geophysics Report 37: 1–144.

McGANN, G. J., 1976. The environment of deposition of the Wooramel Group (Lower Permian), Lyons River area, Carnarvon Basin, Western Australia. Journal of the Royal Society of Western Australia 59: 47–54.

McWHAE, J. R. J., PLAYFORD, P. E., LINDNER, A. W., GLENISTER, B. F. & BALME, B. E., 1958. The stratigraphy of Western Australia. Journal of the Geological Society of Australia 4 (2): 1–161.

NALIVKIN, D. V., 1979. Brakhiopody Turneiskogo Yarusa Urala. Nauka, Leningrad, 284 p.

RAGGAT, H. G., 1936. Geology of Northwest Basin, Western Australia, with particular reference to the stratigraphy of the Permo-Carboniferous. Journal and Proceedings of the Royal Society of New South Wales 70: 100–174.

TEICHERT, C., 1952. Carboniferous, Permian, and Jurassic in the Northwest Basin, Western Australia. XIXe Congres Geologique International: Alger 1952. Symposium sur les Series de Gondwana, 115–135.

VAN DE GRAAFF, W. J. E., HOCKING, R. M. & DENMAN, P. D., 1977. Revised stratigraphic nomenclature and interpretations in the east-central Carnarvon Basin, WA. Geological Survey of Western Australia Annual Report (1976): 37–39.

WATERHOUSE, J. B. & RAO, A. R., 1989. Early Permian brachiopod and molluscan species from the Bap Formation of Peninsular India. Paläontologische Zeitschrift 63: 25–39.

THE EFFECT OF LOW ROOT TEMPERATURES ON THE GROWTH OF MOUNTAIN FOREST EUCALYPTS IN RELATION TO THE ECOLOGY OF *EUCALYPTUS NITENS*

E. A. Chesterfield[1], M. J. McCormick[2] and G. Hepworth[3]

[1]National Parks and Public Land Division, and [2]Natural Resource Systems Division, Department of Conservation and Environment, PO Box 41, East Melbourne, Victoria 3002
[3]Biometric Services, Department of Agriculture, PO Box 500, East Melbourne, Victoria 3002

Chesterfield, E. A., McCormick, M. L. & Hepworth, G., 1991:12:31. The effect of low root temperatures on the growth of mountain forest eucalypts in relation to the ecology of *Eucalyptus nitens*. *Proceedings of the Royal Society of Victoria* 103 (2): 67–76. ISSN 0035-9211.

To compare the response of four montane eucalypts to low soil temperature, seedlings of *Eucalyptus regnans, E. delegatensis, E. fastigata* and four provenances of *E. nitens* were treated for 100 days in a glasshouse. Mean ambient air temperatures varied between 15°C and 29°C while temperatures within the root zone were held in the vicinity of either 5°C or 10°C.

All species grew significantly better at the higher temperature for all variables measured. Differences in stem diameter, root length, root and shoot dry weight were consistent between species at both temperatures. Growth of *E. regnans* and *E. nitens* was similar overall. For most variables both species grew significantly better than *E. delegatensis*, which grew significantly more than *E. fastigata*. For height growth there was a highly significant interaction between species and temperature. At both temperatures, *E. regnans* made significantly better height growth than all other species. At the higher temperature, *E. fastigata* grew significantly taller than *E. nitens* and *E. delegatensis* but, at the lower temperature, *E. nitens* grew significantly taller than *E. delegatensis* and *E. fastigata*. Comparing the difference in height growth, *E. fastigata* and *E. delegatensis* were reduced substantially more than *E. nitens* by the cool root environment.

Eucalyptus nitens has a restricted distribution for a species with outstanding vigour. This may be related to a fire regime which also encourages the development of rainforest understories, and cool, heavily shaded soils. The implications of topography and fire regime on understorey type and soil temperature are discussed in relation to the ecology of *E. nitens*.

FOUR TALL forest eucalypts in the mountain forests of southeastern Australia have overlapping distributions in regions with mean annual rainfall exceeding 750 mm. *Eucalyptus delegatensis* R. Baker and *E. regnans* F. Muell are dominant species over extensive highland areas of Tasmania and Victoria (Eldridge 1972, Boland & Dunn 1985). *E. delegatensis* extends into southern New South Wales, replacing *E. regnans* above 1000 m over the greater part of its range. *E. nitens* (Deane & Maiden) Maiden and *E. fastigata* Deane & Maiden occupy similar latitudes in northern New South Wales (Sherry & Pryor 1967, Tibbits & Reid 1987). Both species extend south into East Gippsland, Victoria, while scattered stands of *E. nitens* also occur westward along the Great Dividing Range and into the Central Highlands. The elevation range of both species is influenced by latitude but, in Victoria, optimum development occurs at or near the lower limit of winter snow.

The growth rates of *E. nitens* are recognised as being greater than those of *E. regnans* in plantations up to 15 years (Pedrick 1976), and planting trials indicate that *E. nitens* can be successfully grown in cool mountain areas receiving an annual rainfall of over 1000 mm (Turnbull & Pryor 1978). Despite this, the natural distribution consists mainly of small, disjunct stands (Pederick 1979) that may be enclaves of formerly more widespread populations.

Three broad regional forms of *E. nitens* have been recognised on the basis of leaf shape (Shepherd et al. 1976). The northern New South Wales form occurs near Mt Ebor and Barrington Tops. The southern New South Wales and West Gippsland forms both occur in Victoria. They differ in their morphology and vigour (Pederick 1979) and in some aspects of their physiology (Pederick & Lennox 1979, Tibbits & Reid 1987). The West Gippsland form is fast growing with strongly glaucous juvenile leaves and occurs

predominantly in the Central Highlands. The southern New South Wales form is less glaucous, less vigorous and has marginal glands on its mature leaves. The major occurrence of this form is on Errinundra Plateau. It also occurs intermixed with the West Gippsland form on the western slopes of the Baw Baw Ranges and on the Toorongo Plateau; however, the West Gippsland form does not occur naturally in East Gippsland.

In the Victorian Central Highlands, *E. nitens* is often found in association with or in close proximity to the cool temperate rainforest species *Nothofagus cunninghamii* (Hook.) Oerst. and *Atherosperma moschatum* Labill. Mixed forest associations with *Elaeocarpus holopetalus* F. Muell and *A. moschatum* replace *N. cunninghamii* in East Gippsland beyond the natural range of that species. In areas where the understorey consists of a dense growth of *A. moschatum, E. holopetalus* and associated cool temperate closed forest species, an almost complete dominance of the site by *E. nitens* is often apparent. In northern New South Wales, mixed forest reoccurs with associations between *E. nitens* and *Nothofagus moorei* (F. Muell) Krasser (Pederick 1977).

The development of cool temperate closed forest understorics has been associated with crown die-back in mature *E. delegatensis* forest in Tasmania (Ellis 1964, 1971, Ellis et al. 1980) although associated *E. dalrympleana* Maiden was unaffected. Ellis et al. (1980) concluded that depressed root temperatures due to the encroachment of closed forest may be important in the "decline" of *E. delegatensis*, as the deterioration could be reversed by cutting or burning the understories. A mean annual soil temperature below 7°C was identified as the critical point at which the growth of *E. delegatensis* deteriorated (Ellis 1971). Although healthy and unhealthy stands differed little in winter soil temperatures, unhealthy stands had summer temperatures below 10°C. This suggested that soil temperature could be an important factor influencing the natural distribution of eucalypts (Ellis 1971).

The strong topographic and floristic similarities between the declining *E. delegatensis* forests of Tasmania and the apparently unaffected *E. nitens* forests of Errinundra Plateau suggested that *E. nitens* might be more tolerant of low soil temperatures than *E. delegatensis*. This factor might also influence the distribution of *E. regnans* and *E. fastigata* in eucalypt–rainforest associations in Victoria. The aim of this study was to test this experimentally under controlled conditions.

METHOD

To investigate the effect of lowered root temperatures on eucalypts occurring in the montane zone and likely to form an association with a rainforest understorey, seedlings of four common montane eucalypts were grown at temperatures near that identified by Ellis (1971) as critical to the onset of die-back. Seedlings for the trial were grown from provenances listed in Table 1. Seeds of *E. nitens* were collected from several trees at each provenance and care was taken to distinguish between the southern New South Wales and West Gippsland forms at Mt Toorongo. Seeds of *E. delegatensis, E. fastigata* and *E. regnans* came from bulked seed lots and

Species	Locality	Latitude	Longitude	Elevation (m.a.s.l)	Form
E. nitens	Royston River, Central Highlands	37° 25′	146° 53′	1000	West Gippsland (CR)
E. nitens	Mt Toorongo, Central Highlands	37° 50′	146° 07′	1200	West Gippsland (CT)
E. nitens	Mt Toorongo, Central Highlands	37° 49′	146° 07′	1000	Southern NSW (ET)
E. nitens	W Errinundra, East Gippsland	37° 19′	148° 52′	1000	Southern NSW (EE)
E. delegatensis	Delegate River, East Gippsland	37° 17′	148° 50′	1000	East Gippsland
E. fastigata	Delegate River, East Gippsland	37° 17′	148° 50′	1000	East Gippsland
E. regnans	Nunnet, East Gippsland	37° 14′	148° 05′	1000	East Gippsland

Table 1. Eucalypt species and provenance.

would have included a greater number of parent trees.

A selection of uniformly large seeds was germinated on moist plugs of sterile rock fibre. *E. delegatensis* was sown after 6 weeks stratification at 4°C. Because of greater growth rate of seedlings, seeds of all other species were sown one month later. Five seeds were sown in each plug. After germination each plug was placed on the top of a 250 mm length of 60 mm diameter PVC pipe filled with clean river sand. The seedlings were kept moist in a shade house by spray irrigation and fertilized every third day with 10 mL of water and 10 mL of Duralite Hysol, a complete hydroponic nutrient solution. Once established, the seedlings were thinned to leave one plant within each growth tube.

After 115 days from the first sowing, the plants were transferred to an empty glasshouse where they were temporarily stored on the floor. After measuring plant height, ten individuals of each provenance were randomly chosen for initial dry weight and root length determination. At this stage the *E. nitens* seedlings developed a light infection of powdery mildew. All plants were elevated on benches and given two applications of TILT (Ciba-Geigy), a wide spectrum Triazole derivative systemic fungicide at a five day interval. Within ten days there was no evidence of active infection. The plants were given a further 20 days to recover and acclimatise to the glasshouse before the cool root treatment was applied. During this period all seedlings were showing healthy and apparently unaffected new growth. The *E. delegatensis* seedlings were therefore 145 days old at the commencement of the experiment.

Two root temperatures were replicated three times, in six forced air coolers. Mean warm root temperatures were maintained between 8.5°C and 10.5°C while mean cool root temperatures were maintained between 4.5°C and 6.5°C. Temperatures were measured using mercury thermometers inserted to a depth of 75 mm at both ends of the cooler. The treatments were arranged down the centre of the glasshouse so that the different root temperatures were adjacent. Five plants of each of seven provenances were allocated at random to each of the six coolers. The plants were evenly distributed with their centres 110 mm apart.

The growth tubes were suspended through a false lid so that the roots in each tube were surrounded by fan-circulated air at controlled temperature, while the aerial parts of each plant were exposed to the ambient temperature of the glasshouse. A small temperature gradient of approximately 1°C existed across each cooler, and small differences in the operation of thermostats meant that the regulation of root temperature differed slightly between coolers. To compensate, lids were moved between coolers and turned once through 180° within each cooler so that, as far as possible, all plants experienced an equivalent root and shoot environment.

Temperature control in the coolers was adequate to ensure that clear differences existed between treatments and that similar temperatures were maintained between replicates (Table 2). Some difficulties were experienced in adjusting the thermostat in cooler 1 and the cooler was replaced after 16 days. Cooler 6 failed over a weekend and was replaced the following Wednesday. Typically, temperature fluctuates in the upper soil horizons both diurnally and annually, and lags behind air temperature. Experimentally maintained constant temperatures do not mimic most natural situations, although they may be more typical of soils protected by dense, rainforest vegetation. Watson (1980) considered that soils above 400 m elevation of the Great Dividing Range of Victoria are likely to have a mean annual temperature between 8°C and 15°C. On Errinundra Plateau at mid morning in mid November, soil temperatures of 7–8°C were obtained using a mercury thermometer at 130 mm depth, beneath dense rainforest vegetation. It is therefore conceivable that the experimental

Treatment Temp (°C)	Cooler	Period			
		May/June (°C)	July (°C)	Aug/Sept (°C)	May/Sept (°C)
10°C	1	9.8–12.5	8.6–9.5	8.9–9.6	9.1–10.5
	3	9.6–10.7	8.2–9.4	8.5–9.6	8.8–9.9
	5	9.4–11.8	8.5–9.4	8.8–9.9	8.9–10.4
5°C	2	4.8–6.3	4.5–6.7	4.8–6.1	4.7–6.4
	4	5.1–6.1	4.4–5.0	5.0–6.0	4.8–5.7
	6	6.2–7.4	4.6–5.5	4.4–5.8	5.1–6.2

Table 2. Mean minimum and maximum soil temperature in each cooler.

temperatures could be experienced naturally by the species involved in the trial.

The root medium was washed with water and the plants fertilized to excess every second or third day, initially with 60 mL of nutrient solution, then with 120 mL as they increased in size. Glasshouse temperature and humidity were monitored by a continuous recording thermo-hydrograph. Occasional roots extending beyond the growth tubes were clipped and stored in an alcohol and formalin mixture. Fallen leaves were collected for dry weight determination.

The trial ran for 100 days after which plants were measured for diameter at the harvest point (Dia) and total height (Ht). After harvest, the roots were placed on a fine wire mesh and washed free of sand by a gentle spray and hand teasing, with final cleaning of attached sand grains by forceps. They were stored in an alcohol/formalin mixture for root length determination. Total root length (RL) was determined using a Comair Rootlength Scanner (Richards et al. 1979). Root lengths estimated to be greater than 100 m were partitioned for separate measurement. Roots and shoots were held at 65°C for five days and dry weights of root and shoot (Dwt(r), Dwt(s)) were determined after stabilising for 1 hour at room temperature.

RESULTS

Mean monthly air temperature and relative humidity in the glasshouse during the trial (Table 3) were uniform, with a diurnal fluctuation in mean maximum and minimum temperature of 10°C and in relative humidity of

approximately 20–30%. Absolute maximum and minimum temperatures of 37.7°C and 11.2°C were recorded.

Increment in growth was obtained by subtracting initial values for each plant in the case of height, and means of an initial sample for root length and dry weight of roots and shoots. An analysis of variance showed all variables to be significantly affected by temperature (Table 4), with growth reduced at the lower soil temperature, as expected.

Height was the only variable for which a temperature × species interaction was significant and this was highly significant (Table 4). At the higher temperature, height growth of *E. regnans* and *E. fastigata* was significantly greater than *E. nitens* and *E. delegatensis* (p < 0.01) which were not significantly different from each other. At the lower root temperature, height growth of *E. nitens* was significantly greater than that of *E. delegatensis* or *E. fastigata* (p < 0.001). At 5°C, height growth of both *E. delegatensis* and *E. fastigata* was ca. 60% less than that at 10°C. In contrast the height reduction in *E. regnans* and *E. nitens* was ca. 30% or less (Table 5). *Eucalyptus regnans* achieved much better height growth at both temperatures at this age than all other species (Table 5). At both temperatures, the southern New South Wales form of *E. nitens* grew significantly better than the West Gippsland form (p < 0.01), and within forms there was no significant difference between provenances.

A comparison of shoot to root ratios at the two temperatures (Table 6) suggests that *E. nitens* and *E. regnans* differed from *E. delegatensis* and *E. fastigata* in their ability to maintain stronger shoot growth relative to root growth at the lower

Period	Mean Temperature (°C)		Mean Relative Humidity %	
	Maximum	Minimum	Maximum	Minimum
May–June	26.5	16.5	67.0	43.1
July	27.2	17.6	67.3	46.4
Aug–Sept	29.1	15.1	72.7	40.6

Table 3. Mean monthly air temperatures and relative humidities in the glasshouse.

Variable	Height	Diameter	Root Length	Dry Weight Shoot	Dry Weight Root	Dry Weight Total
Temp.	0.007	0.023	<0.001	0.011	0.005	0.009
Temp. × Species	<0.001	0.353	0.433	0.893	0.342	0.822

Table 4. Probability values from analysis of variance testing the effect of soil temperature and temperature/species interactions. The main effect of species was significant at p < 0.001 for all variables.

Species	Mean Height Increment (mm) Soil Temperature		Percentage Reduction in Height Growth with fall in Soil Temperature
	5°C	10°C	
E. nitens CR	299	440	32
E. nitens CT	277	403	31
E. nitens EE	364	500	27
E. nitens ET	395	481	18
E. regnans	436	630	31
E. delegatensis	160	406	61
E. fastigata	204	546	63
Least Significant Difference	67	66	

Table 5. Comparison of mean shoot height increment (mm) during the experimental period at two soil temperatures.

Species	Shoot(g)/Root(g) Soil Temperature			Shoot (mm)/Root (m) Soil Temperature		
	5°C	10°C	Difference	5°C	10°C	Difference
E. nitens CR	4.5	4.0	0.5	2.8	2.5	0.3
E. nitens CT	4.9	4.6	0.3	5.2	4.1	1.1
E. nitens EE	4.5	4.7	−0.2	5.2	4.7	0.5
E. nitens ET	4.2	3.9	0.3	5.1	4.1	1.0
E. regnans	5.2	4.6	0.6	6.9	4.9	2.0
E. delegatensis	3.8	4.2	−0.4	2.5	3.9	−1.4
E. fastigata	3.6	4.1	−0.5	6.8	7.2	−0.4

Table 6. Ratio of mean shoot to root dry weight growth and increment in length, and their differences at the two soil temperatures.

temperature. Comparatively low and high root lengths were responsible for the high and low length ratios for *E. fastigata* and the Royston provenance of the West Gippsland (CR) form of *E. nitens* respectively.

For those variables where there was no significant interaction between species and temperature, the data from the different temperatures were combined to determine the significance of difference between species (Table 7). *E. nitens* overall grew significantly better (p < 0.05) than *E. delegatensis* for all variables, and the growth of *E. delegatensis* was significantly greater than *E. fastigata* for all variables (p < 0.001). The West Gippsland form of *E. nitens* from Royston (CR) grew significantly better than *E. regnans* and the other provenances of *E. nitens* for all variables. *E. regnans* was significantly better than *E. delegatensis* for all variables except root length and basal stem diameter.

Variable Temp°C	Basal Stem Diameter (mm)			Total Root Length (mm)			Shoot Dry Weight (g)			Root Dry Weight (g)			Total Dry Weight (g)		
	5°	10°	Mean	5°	10°	Mean	5°	10°	Mean	5°	10°	Mean	5°	10°	Mean
E. nitens CR	0.54	0.60	0.57	108	173	141	5.97	8.77	7.37	1.33	2.20	1.77	7.31	10.96	9.14
E. nitens CT	0.43	0.54	0.48	53	99	76	3.40	5.89	4.65	0.70	1.27	0.99	4.10	7.16	5.63
E. nitens EE	0.46	0.55	0.51	70	106	88	4.73	6.97	5.85	1.05	1.48	1.27	5.79	8.45	7.12
E. nitens ET	0.51	0.57	0.54	77	117	98	5.09	7.31	6.20	1.20	1.87	1.54	6.29	9.19	7.74
E. regnans	0.44	0.52	0.48	63	129	84	4.57	7.63	6.15	0.87	1.66	1.28	5.44	9.30	7.44
E. delegatensis	0.38	0.51	0.45	64	103	84	2.98	5.64	4.31	0.79	1.33	1.06	3.77	6.97	5.37
E. fastigata	0.27	0.40	0.33	30	76	53	1.46	3.53	2.46	0.41	0.87	0.63	1.88	4.40	3.10
Least Significant Difference			0.04			17			0.80			0.21			0.98

Table 7. Mean growth at each soil temperature for variables in which the species × temperature interaction was not significant, and combined temperature means for each species.

DISCUSSION

Although the effect of low root temperatures has been widely researched in horticulture (e.g. Cooper 1973, Nielsen & Humphries 1966), the implications of low soil temperatures on growth have received little consideration in the study of natural ecosystems. Low soil temperatures influence the formation of mycorrhizal associations (Theodorou & Bowen 1970) and increase the resistance to the uptake of nutrients (Kramer 1969). In particular, phosphorus is absorbed much more slowly at low than at high temperatures (Sutton 1969). Paton et al. (1979) observed the effect of root temperature on dehardening of four species of eucalypts and found that root temperature in the range 0.5–1.0°C delayed the dehardening response of warm shoots. In general, below the optimum temperature, height growth, root length and dry weight production show a broad sigmoidal increase with increasing temperature to an optimum, beyond which further temperature increase causes a decline in productivity. In most trials of horticultural or agricultural species, the optimum band of root temperature differed between species but was between 20–30°C. In this trial, root temperatures were probably well below optima for all species.

The significant interaction between species and temperature for height growth in this trial was not evident for the other variables tested. Eucalypts that compete with vigorous shrub growth in the early stages of establishment must make rapid, early height growth if they are to survive. In contrast, diameter growth changes little, particularly during the seedling stages. Thus height growth of seedlings may be more sensitive to the different root temperature regimes than the other variables tested. A similar discrepancy between height growth and dry weight production was recorded for *Pinus radiata* and *Pinus contorta* by Sweet & Wareing (1968). Dry weight of their second year seedlings was almost identical for the first eight months, despite more than 30% difference in height growth. In the following months, when the height growth of both species was negligible, dry weight production continued at a reduced rate and clear differences were finally evident in the partitioning of dry weight between root and stem. For the eucalypts tested in this trial, soil temperature appeared to influence this ratio with the response of *E. regnans* and *E. nitens* differing from that of *E. fastigata* and *E. delegatensis*.

The height growth of the southern New South Wales form (EE and ET), which was significantly better than the West Gippsland form (CR and CT), emphasises the difficulties associated with using seedlings as a guide to growth in later stages (Table 5). Pederick (1979) found ranking of provenances according to height growth changed after planting in the field. The Errinundra provenance which was initially the tallest had become the shortest within three years. Thus the growth of seedlings in containers is at best a poor guide to the response of mature to over mature trees growing in the natural environment.

Major Victorian occurrences of *E. nitens* are on plateaus. At the time of European settlement the most extensive populations of *E. nitens* occurred on Errinundra Plateau and Toorongo Plateau. Where the species occurs amongst more steeply dissected land forms, it is often confined to depressions, gully heads or on moderate slopes, in contrast to forests of surrounding species, eg. Connors Plains, Mt Useful Spur, headwaters of Snobs Creek, Moroka, Royston, Rubicon, Little and Taggerty Rivers, Torbreck Range (Pederick 1977) and slopes below the Baw Baw Plateau, e.g. Christmas Creek.

Plateau topography affects at least two factors that influence the vegetation. The undulating landform may increase the severity of frosts through cold air drainage, and by influencing the rate of fire spread, plateaus may reduce fire intensity and frequency.

Where the effect of frost is regular and pronounced it may delimit the tree line (Moore & Williams 1976). Rare but exceptionally severe frosts may influence the segregation of species (Davidson & Reid 1985), particularly amongst lower growing species. For tall growing eucalypts, frost effects are likely to be most severe during early establishment stages. Superior frost resistance combined with good growth rate has led to the increasing significance of *E. nitens* as a plantation species in Tasmania (Tibbits 1986) and in other countries (Tibbits & Reid 1987). High frost frequency on Errinundra Plateau could be at least partly responsible for that extensive occurrence of *E. nitens* (Featherstone et al. 1987), although a comprehensive study of variation in frost resistance indicated that the southern New South Wales and Errinundra provenances of *E. nitens* were least frost hardy (Tibbits & Reid 1987). Damage due to frost would be most pronounced during early regeneration stages, particularly if regeneration occurred as even aged stands without the pro-

tection of an overwood. Since 1967, 4800 ha of forest have been logged by clear felling on Errinundra Plateau. Because of limited seed production, it has not been possible to regenerate these stands with pure *E. nitens*. Various mixtures of *E. nitens, E. delegatensis* and *E. fastigata* have been used, with extensive areas regenerated by a seed mixture containing equal proportions of all three. To date regeneration of all three species has occurred without a particular problem due to frost.

Because fire intensity is exponentially related to slope (McArthur 1967) fires burn less intensely on plateaus, and possibly less frequently. The multi-aged stands observed in Tasmania (Webb et al. 1983) are favoured on plateaus because fires create favourable seed bed conditions but have less tendency to destroy the overwood, particularly where this consists of mature trees. Forests with these structures have been observed over a long period in *E. regnans* and *E. delegatensis* forests in Victoria and Tasmania (Lindenmayer et al. 1990). Similar structures have been recorded in mixed stands of *E. nitens* and *E. delegatensis* in the headwaters of the Rodger River (Chesterfield et al. 1983), and in *E. nitens* on Errinundra Plateau. Fires in 1939 burnt the margins of Errinundra Plateau and, at one point where the regrowth occurred amongst a scattered stand of *E. nitens*, the multi-aged structure is clearly evident (Chesterfield et al. 1988). More recently, during burning of logging debris on Errinundra Plateau, approximately one hectare of mature forest recovered after complete defoliation by heat scorch. Thus, provided adequate gaps occur, the formation of multi-aged stands is not an improbable event.

The modification of the fire regime by plateau topography that favours the formation of multi-aged eucalypt stands also protects and encourages the development of rainforest in areas where soils and rainfall are adequate. In Victoria, *Atherosperma moschatum, Nothofagus cunninghamii* and *Elaeocarpus holopetalus* are important constituents of the *E. nitens* environment and, in the absence of fire, produce heavily shaded soils at maturity. Forests with similar composition and structure occupy similar environments in Tasmania. Here somewhat uneven aged stands of *E. delegatensis* first declined in the early 1960s, following a period of approximately 140 years without fire. Die-back was associated with the development of dense, closed forest understories. Trees of all age classes and canopy positions were affected and the onset of die-back was influenced by elevation.

Below 750 m, stands with a similar understorey were unaffected. After studying soil chemical factors, Ellis & Graley (1987) concluded that the small differences were more likely to be the result rather than the cause of successional changes. Ellis (1971) initially proposed that temperature changes in the root environment were a possible explanation. Over a two year period he recorded mean annual soil temperatures at a depth of 450 mm which were 2–3°C higher under grass in comparison with the rainforest understorey. After considering the environmental lapse rate he calculated that the rainforest invasion was equivalent to an altitudinal increase of 335–520 m, placing stands at 915 m, well above their altitudinal limit. Although the cause of die-back has not been ascertained with any certainty, the results for height growth in this study support the hypothesis that low soil temperatures may be a factor contributing to the decline in *E. delegatensis*. The natural post fire succession in this forest type is toward understories that are open at maturity and dominated by grasses, forbs, and ferns over the greater part of their range. Heavily shaded soils associated with a closed forest understorey are rarely present.

The similarities between the vegetation, fire regime and successional changes that have occurred on the elevated montane plateaus of Victoria and Tasmania are striking, with the exception that in Victoria, in areas where the rainforest understorey is dense, die-back of the *E. nitens* overstorey has not been observed. It is recognised that *E. nitens* can tolerate the incursion of rainforest species for longer periods than either *E. delegatensis* or *E. regnans* (United Nations Food and Agriculture Organisation 1979).

In the montane forests of southeastern Australia, fires over a wide elevation zone extending above and below the snow line have been sufficiently frequent to favour eucalypt species capable of producing regular and reliable seed crops. Although *E. nitens* has proven to be of equal or superior vigour to most of its competitors in growth trials, it is an unreliable and poor seed producer (United Nations Food and Agriculture Organisation 1979, Turnbull & Pryor 1978, Boland et al. 1980), particularly when compared to *E. regnans, E. delegatensis* and *E. fastigata*. Therefore, as the frequency of fire increases, the proportion of *E. nitens* in mixed stands is likely to decline, as noted in the Rodger River (Chesterfield et al. 1983).

The role of fire in the natural distribution of *E.*

nitens may resemble that of *E. grandis* Maiden, another eucalypt that associates with rainforest genera (Cremer 1960). The natural distribution of *E. grandis* is restricted to moist gullies or tablelands (Turnbull & Pryor 1978) due to its extreme sensitivity to fire (Pryor 1972). In the event of a change in fire regime to provide greater protection, the range of *E. grandis* may be readily extended into adjoining sites. Conversely, an increase in the frequency and intensity of fire would cause a contraction of the range. Ashton (1981) considered that during the Pleistocene fires may have been much rarer events than at present, and that the wet sclerophyll forests may have been relatively scarce ecotones between rainforests and the more drought resistant eucalypt forests or woodlands. As fire increased with increasing aridity during the early Quaternary, the contraction of rainforest may have enlarged the ecotone as fire reduced or modified rainforest over the greater part of its range. Some species of *Eucalyptus, Tristaniopsis* and some rainforest genera adapted to regenerate following disturbance, or on marginal sites, e.g. *Araucaria, Flindersia* (Cromer & Pryor 1942), may have dominated this ecotone. The co-existence of eucalypts with cool temperate closed forest has been suggested in areas of Tasmania where fire is infrequent but sufficiently frequent (intervals less than 350 years) to maintain the eucalypts (Gilbert 1959). Thus the fire regime during the early Quaternary may have contributed to vegetation with similar structure to the mixed forest surviving on Errinundra Plateau, and in other isolated montane and coastal forests of southeastern Australia.

After the arrival of the Aborigines, a sudden and dramatic increase in fire frequency may have allowed eucalypts to expand into moister sites that they had not formerly occupied (Smith & Guyer 1983). In southeastern Australia, species belonging to the subgenus *Monocalyptus* are frequently best adapted to such sites (Florence 1981). Their more recent evolution on uniform, regularly watered sites may explain a tendency to form monospecific stands in tall open-forests, lower tolerance to prolonged water stress and their restriction to higher rainfall zones in the south-east and south-west of the continent. The expansion of fire-adapted species may have seen a contraction of rainforest and mixed forest dominated by eucalypts adapted to long intervals between fires. The contraction would have occurred last in the most fire protected localities. In some areas of Victoria,

elevation and topography appears to have been important for the survival of *E. nitens*.

At elevations below the limit of permanent winter snow, *E. nitens* is in competition with *E. regnans* and *E. fastigata* and at higher elevations with *E. delegatensis*. In general, its competitors produce reliable, heavy seed crops and regenerate prolifically after hot fires. In contrast, *E. nitens* produces light and irregular seed crops, and over a long period a series of hot fires could be expected to cause a progressive diminution in its abundance. In competition with *E. regnans*, a species of comparable vigour, the decline in *E. nitens* would be appreciable after each regeneration phase. The ability of *E. nitens* to compete with *E. delegatensis* is limited by the dormancy characteristics of its seed. The stratification requirement of *E. delegatensis* seed indicates an adaptation to an environment where snow may lie for extended periods during winter (Boland et al. 1980). Without this adaptation, the mortality of *E. nitens* germinants would be high, restricting the upper limits of natural establishment to elevations where snow generally persists for less than several weeks. This environment coincides with the extremes in distribution for *E. delegatensis* and *E. regnans*, allowing *E. nitens* to exploit the ecotone where both its competitors are at the limits of their range. The occurrence of plateau land form at this vulnerable point in the elevation gradient of both *E. regnans* and *E. delegatensis* may have protected the niche available to *E. nitens* by a modification of the fire regime. On plateaus, fires occur less intensely and probably less frequently, favouring the development of multi-aged stands. In forests with this structure, poor seed production would have been much less critical to species survival, and competitors promoted by fire less invasive. The fire regime occurring on plateaus also favours the development of rainforest understories. An ability to co-exist at various times for extended periods in this association, may have been a factor in the survival of *E. nitens* on plateau and gully topography in Victoria.

ACKNOWLEDGEMENTS

of Conservation and Environment, Victoria, and by Dr D. Ashton, Melbourne University. We thank Mr F. Morris, Department of Conservation and Environment (retired) for sharing his field experience of *Eucalyptus nitens* and the Errinundra Plateau.

REFERENCES

ASHTON, D. H., 1981. Fire in tall open-forests. In *Fire and the Australian Biota*, A. M. Groves & I. R. Noble, eds, Australian Academy of Science, Canberra, 339–366.

BOHM, W., 1979. *Methods of Studying Root Systems* (*Ecological Studies*, vol. 33, W. D. Billings & O. L. Langer, eds). Springer-Verlag, Berlin, 188 p.

BOLAND, D. J. & DUNN, A. T., 1985. Geographic variation in alpine ash (*Eucalyptus delegatensis* R. T. Baker). *Australian Forest Research* 15: 155–171.

BOLAND, D. J., BROOKER, M. I. H., & TURNBULL, J. W., 1980. *Eucalyptus Seed.* CSIRO, 191 p.

BOWEN, G. D., 1970. Effects of soil temperature on root growth and on phosphate uptake along *Pinus radiata* roots. *Australian Journal of Soil Research* 8: 31–42.

CHESTERFIELD, E. A., MACFARLANE, M. A., ALLEN, D., HUTCHINSON, M. N, TRIGGS, B. & BARLEY, R., 1983. *Flora and Fauna of the Rodger Forest Block, East Gippsland, Victoria.* Ecological Survey Report No. 1, Forests Commission of Victoria.

CHESTERFIELD, E. A., HURLEY, V. A., HENRY, S. R., SCHULZ, M. & PYRKE, A. F., 1988. *Flora and Fauna of the Brodribb Forest Block, East Gippsland, Victoria.* Ecological Survey Report No. 19, Department of Conservation, Forests and Lands Victoria.

COOPER, A. J., 1973. *Root Temperature and Plant Growth.* Commonwealth Bureau of Horticulture and Plantation Crops Research Review No. 4, Commonwealth Agriculture Bureaux, Maidstone, Kent.

CREMER, K. W., 1960. *Eucalypts* in rainforest. *Australian Forestry* 24: 120–126.

CROMER, D. A. N. & PRYOR, L. D., 1942. A contribution to rainforest ecology. *Proceedings of the Linnean Society of New South Wales* 67: 249–268.

DAVIDSON, J. J. & REID, J. B., 1985. Frost as a factor influencing the growth and distribution of subalpine eucalypts. *Australian Journal of Botany* 33: 657–667.

ELDRIDGE, K. G., 1972. *Genetic Variation in Growth of* Eucalyptus regnans. Australian Forestry and Timber Bureau Bulletin No. 46, Australian Government Publishing Service, Canberra.

ELLIS, R. C., 1964. Dieback of alpine ash in north-eastern Tasmania. *Australian Forestry* 28: 75–90.

ELLIS, R. C., 1971. Dieback of alpine ash as related to changes in soil temperature. *Australian Forestry* 35: 152–163.

ELLIS, R. C., MOUNT, A. B. & MATTAY, J. P., 1980. Recovery of *Eucalyptus delegatensis* from high altitude dieback after felling and burning the understorey. *Australian Forestry* 43: 29–35.

ELLIS, R. C. & GRALEY, A. M., 1987. Soil chemical properties as related to forest succession in a highland area in north-east Tasmania. *Australian Journal of Ecology* 2: 307–317.

FEATHERSTONE, G. R., FAGG, P. C. & MORRIS, F., 1987. Climatic features of the Errinundra Plateau, East Gippsland. *Proceedings of the Royal Society of Victoria* 99: 89–97.

FLORENCE, R. G., 1981. The biology of the eucalypt forest. In *The Biology of Australian Plants*, J. S. Pate & A. J. McComb, eds, University of Western Australia Press, Perth, 147–180.

GILBERT, J. M., 1959. Forest succession in the Florentine Valley, Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 93: 129–151.

KRAMER, P. J. 1969. *Plant and Soil Water Relationships.* McGraw-Hill, New York.

LINDENMAYER, D. B., NORTON, T. W. & TANTON, M. T., 1990. Differences between wildfire and clearfelling on the structure of montane ash forests of Victoria and their implications for fauna dependent on tree hollows. *Australian Forestry* 53: 61–68.

MCARTHUR, A. G., 1967. *Fire Behaviour in Eucalypt Forests.* Australian Forestry and Timber Bureau Leaflet No. 107, Australian Government Publishing Service, Canberra.

MOORE, R. M. & WILLIAMS, J. D., 1976. A study of a subalpine woodland–grassland boundary. *Australian Journal of Ecology* 1: 145–153.

NEUMANN, F. G., KASSABY, F. Y. & MCKIMM, R. J., 1975. Defoliation of *Eucalyptus nitens* on the Errinundra Plateau, Orbost district. 1. First progress report. Research Branch Report No. 70, Forests Commission of Victoria. (Unpublished report held in library, Department of Conservation & Environment Victoria.)

NIELSEN, K. F. & HUMPHRIES, E. C., 1966. Effects of root temperature on plant growth. *Soils and Fertilisers* 29: 1–7.

PATON, D. M., SLATTERY, H. D. & WILLING, R. R., 1979. Low root temperature delays dehardening of frost resistant Eucalyptus shoots. *Annals of Botany* 43: 123–124.

PEDERICK, L. A., 1976. *The Genetic Resources of the Victorian Eucalypts.* Bulletin No. 22, Forests Commission of Victoria.

PEDERICK, L. A., 1977. Natural variation in shinning gum, *Eucalyptus nitens.* 1. Growth rate and foliage characteristics, to age 3 years. Unpublished Report, Forests Commission of Victoria. (Held in library, Department of Conservation & Environment Victoria.)

PEDERICK, L. A., 1979. Natural variation in shining gum (*Eucalyptus nitens*). *Australian Forest Research* 9: 41–63.

PEDERICK, L. A. & LENNOX, F. G., 1979. Variation in polyphenolic constituents of *Eucalyptus nitens* Maiden. *Australian Journal of Botany* 27: 217–226.

PRYOR, L. D., 1972. The selection of eucalypts for regeneration. *Australian Pulp and Paper Industry Technical Association* (APPITA) 26: 35–38.

RICHARDS, D., GOUBRAN, F. H. GARWOLI, W. N. & DALY, M. W., 1979. A machine for determining root length. *Plant and Soil* 52: 69–76.

SHEPHERD, K. R., BANKS, J. C. G & ATYEO, W. J., 1976. Variation in *Eucalyptus nitens* Maiden in response to temperature and seed source. *Australian Journal of Botany* 24: 167–176.

SHERRY, S. P. & PRYOR, L. D., 1967. Growth and differential frost-resistance of topoclinal forms of *Eucalyptus fastigata* D. & M. planted in South Africa. *Australian Forestry* 31: 33–44.

SMITH, J. M. B. & GUYER, I. J., 1983. Rainforest-eucalypt forest interactions and the relevance of the biological nomad concept. *Australian Journal of Ecology* 8: 55–60.

SUTTON, P. D., 1969. The effect of low soil temperature on P. nutrition of plants – a review. *Journal of the Science of Food and Agriculture* 20: 1–3.

SWEET, G. B. & WAREING, P. F., 1968. A comparison of the seasonal rates of dry matter production of three coniferous species with contrasting patterns of growth. *Annals of Botany* 32: 721–734.

THEODOROU, G. & BOWEN, G. D., 1970. Influence of temperature on the mycorrhizal associations of *Pinus radiata* D. Don. *Australian Journal of Botany* 19: 13–20.

TIBBITS, W. N. 1986. Eucalypt plantations in Tasmania. *Australian Forestry* 49: 219–225.

TIBBITS, W. N. & REID, J. B., 1987. Frost resistance in *Eucalyptus nitens* (Deane & Maiden) Maiden: genetic and seasonal aspects of variation. *Australian Forest Research* 17: 29–47.

TURNBULL, J. W. & PRYOR, L. D., 1978. Choice of species and seed sources. In *Eucalypts for Wood Production*, W. E. Hillis & A. G. Brown, eds. CSIRO. 6–65.

UNITED NATIONS FOOD AND AGRICULTURE ORGANISATION, 1979. *Eucalypts for Planting*. FAO Forestry Series No 11, Rome, 677 p.

WATSON, G. L., 1980. Seasonal soil temperature regimes in south eastern Australia. *Australian Journal of Soil Research* 18: 325–331.

WEBB, D. P., ELLIS, R. C. & HALLAM, P. M., 1983. *Growth Check of* Eucalyptus delegatensis *(R. T. Baker) Regeneration at High Altitudes in North Eastern Tasmania*. Information Report 0-x-348, Great Lakes Forest Research Centre, Canadian Forestry Service.

THE TASMANIAN MUDFISH, *GALAXIAS CLEAVERI* SCOTT, 1934, IN VICTORIA

J. D. Koehn and T. A. Raadik

Freshwater Ecology Branch, Department of Conservation and Environment, 123 Brown Street, Heidelberg, Victoria 3084

Koehn, J. D. & Raadik, T. A., 1991:12:31. The Tasmanian mudfish, *Galaxias cleaveri* Scott, 1934, in Victoria. *Proceedings of the Royal Society of Victoria* 103 (2): 77–86. ISSN 0035-9211.

Galaxias cleaveri Scott, 1934 is recorded for the first time from the Aire River basin in western Victoria, extending the known westerly distribution of the species. The habitat, general biology and behaviour of the species are described and comparisons made with three species of New Zealand mudfish (*Neochanna* spp.). *G. cleaveri* is nocturnal and able to survive periods without free surface water. Large areas of potential *G. cleaveri* habitat have been destroyed in Victoria, and the preservation of freshwater wetland habitats is essential to the survival of the species in this State, where a conservation status of vulnerable remains justified.

THE TASMANIAN MUDFISH, *Galaxias cleaveri* Scott, a member of the southern hemisphere family Galaxiidae, is a scaleless salmoniform fish first described from Tasmania in 1934 although specimens had been dug up at Strahan in western Tasmania in 1900 (Hall 1901, Scott 1934). The species was considered endemic to Tasmania until 1980 when specimens were discovered on mainland Australia (Jackson & Davies 1982). In the 56 years since its discovery *G. cleaveri* has been recorded only spasmodically, an indication that it is rare in terms of distribution and abundance. Consequently little is known of the general biology and ecology of this species; indeed, not until 1986 did anyone report that it possesses a marine larval stage (Fulton 1986). In the present paper we highlight the presence of *G. cleaveri* in Victoria and provide updated information to help further work and the development of management strategies.

Detailed descriptions of *G. cleaveri* were given by Andrews (1976), McDowall & Frankenberg (1981) and Cadwallader & Backhouse (1983), and the last authors provided a colour photograph. Even so, workers less skilled in the taxonomy of fish may experience difficulty in distinguishing *G. cleaveri* from the broad-finned galaxias, *Galaxias brevipinnis* Günther, and the mountain galaxias, *Galaxias olidus* Günther, which may occur within the same river system.

The following morphological features may be used as a simplified guide to distinguishing adult *G. cleaveri* from *G. brevipinnis* and *G. olidus* (Fig. 1).

1. Anal fin slightly behind origin of dorsal fin in *G. cleaveri*.
2. Shape of dorsal and anal fins: low, rounded to ovoid, elongated posteriorly in *G. cleaveri*.
3. Shape of caudal fin: rounded to truncated in *G. cleaveri*.
4. Shape of flanges on caudal peduncle: large, long and raised in *G. cleaveri*.
5. Shape of pectoral fins: large and rounded in *G. cleaveri*.
6. Small head in *G. cleaveri*.
7. Size of eyes: small in *G. cleaveri*.
8. Large long tubular nostrils: more pronounced in *G. cleaveri*.

Morphological similarities are exhibited with three species of New Zealand mudfish (McDowall & Whitaker 1975, McDowall 1990): the Canterbury mudfish, *Neochanna burrowsius* (Phillipps) (Skrzynski 1968, Cadwallader 1975); the brown mudfish, *N. apoda* Günther (Eldon 1968, 1971); and the black mudfish, *N. diversus* Stokell (Thompson 1987, McDowall 1990). In habitat and habits *G. cleaveri* shows similarities to these species and to the dwarf galaxias, *Galaxiella pusilla* (Mack) (Backhouse & Vanner 1978, Beck 1985, Humphries 1986).

DISTRIBUTION

Previous records

G. cleaveri has been found to be patchily distributed in coastal areas in the north, south and west of Tasmania (Andrews 1976, McDowall & Frankenberg 1981, Fulton 1990) but was reported to be absent from Flinders and King
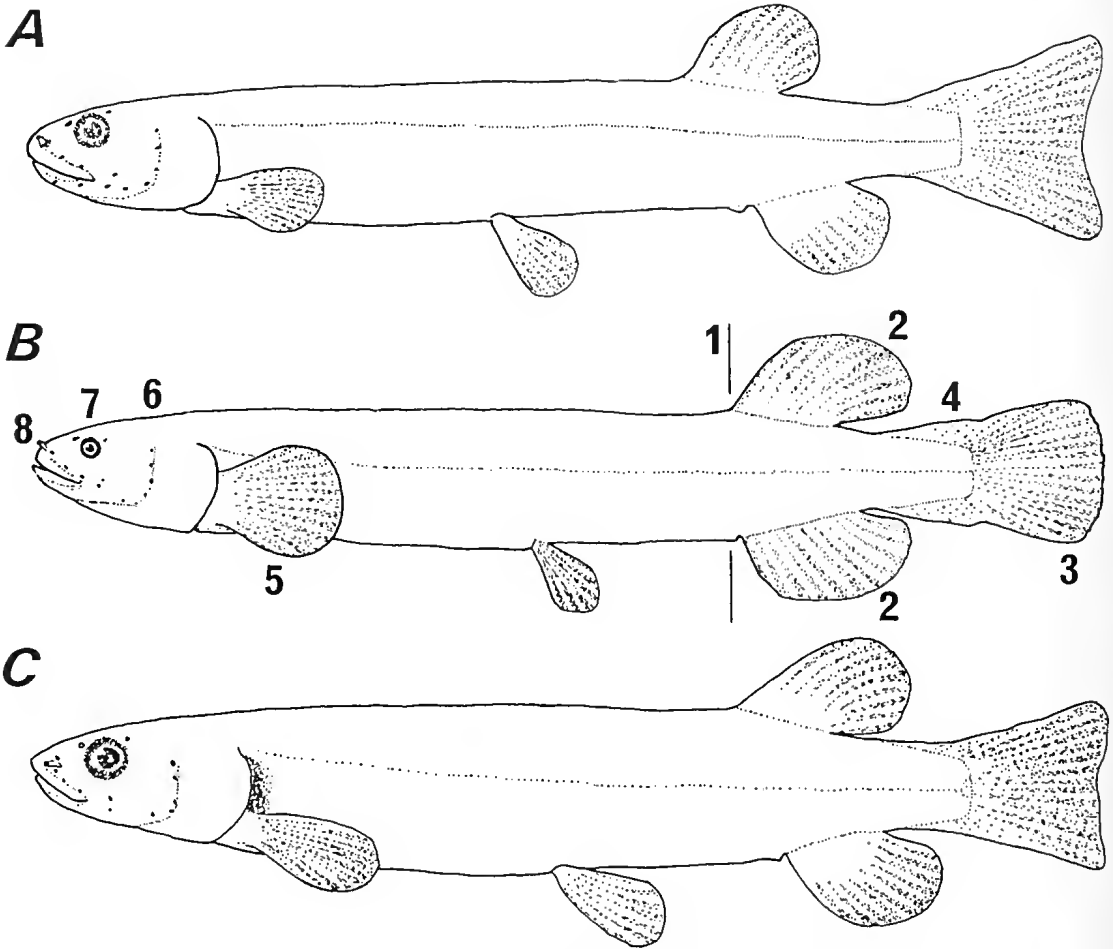
Figure 1. Morphological features distinguishing *Galaxias cleaveri* (B) from *G. olidus* (A) and *G. brevipinnis* (C). (After McDowall & Frankenberg 1981.)

Islands in the 1960s (Frankenberg 1967). Andrews (1976) was surprised at the absence of *G. cleaveri* from the Bass Strait islands and mainland Australia, even though at that time he did not know that the species possessed a marine juvenile stage.

G. cleaveri was first recorded on mainland Australia in 1980 from the south-east side of Wilsons Promontory, Victoria (Jackson & Davies 1982). In 1983 another individual was recorded from the lower reaches of the Wye River, Otway Ranges (Koehn & O'Connor 1990a; specimen NMV A7594, Department of Ichthyology, Museum of Victoria, Melbourne), extending the known range of the species into western Victoria. These two sites are referred to herein as sites 1 and 2 (Fig. 2, Table 1).

Subsequently, Green (1984) reported *G. cleaveri* from a drain on Flinders Island, Bass Strait (specimens QVM 1984/5/6, Queen Victoria Museum and Art Gallery, Launceston, and NMV A3391). This record completed a distribution pattern coinciding with that of other galaxiid species having a trans-Bassian distribution, namely *G. brevipinnis, G. maculatus* (Jenyns), *G. truttaceus* (Valenciennes) and *Galaxiella pusilla* (Frankenberg 1967).

It is not surprising that *G. cleaveri* has been recorded in only two of the numerous other surveys previously conducted to determine the distribution of freshwater fish in coastal Victoria (see Koehn 1990, Koehn & O'Connor 1990a, Koehn et al. 1991). Sites sampled during those surveys were mostly in streams rather than in
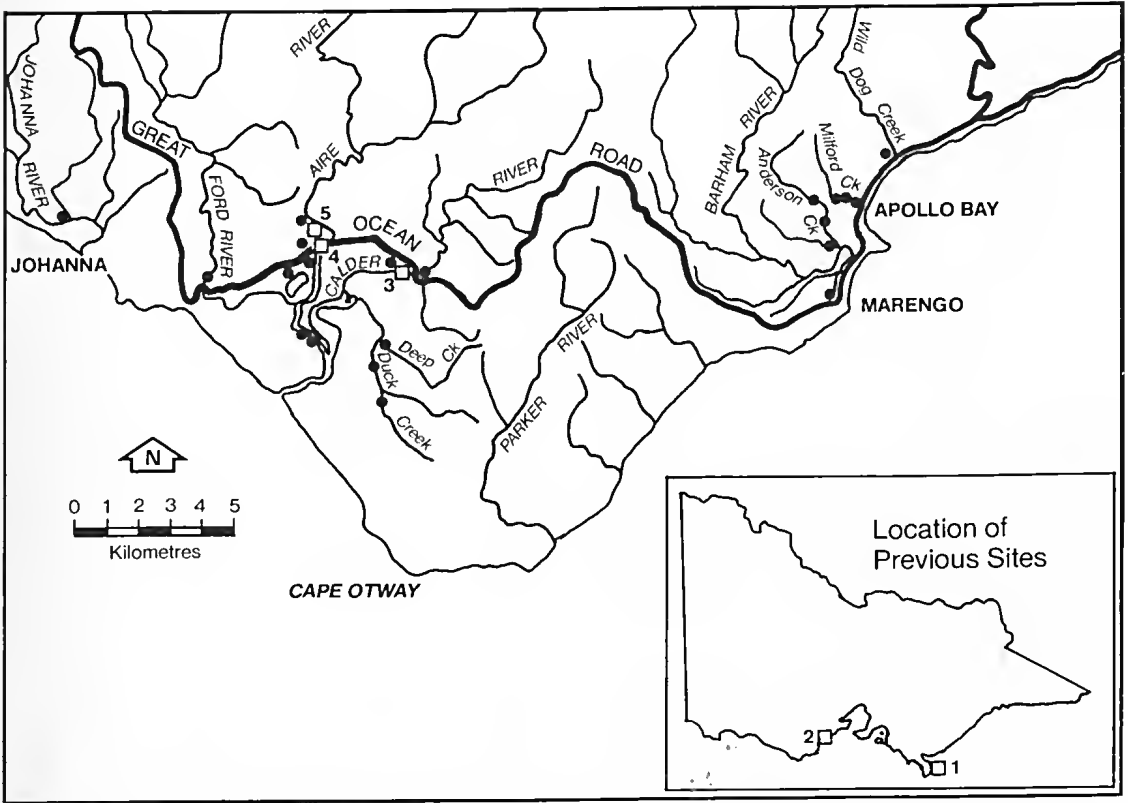
Figure 2. Localities from which *Galaxias cleaveri* has been recorded in Victoria (□); ● = additional sites surveyed in this study, but where *G. cleaveri* was not found. Inset: areas where *G. cleaveri* was previously recorded by Jackson & Davies (1982) (1) and Koehn & O'Connor (1990a) (2).

swamp and drain habitats favoured by this species. In addition, specimens of *G. cleaveri* may have been misidentified, particularly before the species was recognised as occurring in Victoria.

New records

In 1990 we surveyed likely *G. cleaveri* habitats (small creeks, drains and swamps) in the lowland coastal plains of the Otway Ranges between Skenes Creek (143°43'E, 38°43'S) and the Johanna River (143°23'E, 38°45'S) (Fig. 2). Twenty-four sites were sampled using a Smith Root Model 12 backpack electrofisher and dip nets. Details of all sites sampled and fish species collected are included in Koehn et al. (1991). Eleven specimens of *G. cleaveri* were collected from three sites (sites 3, 4 and 5; Fig. 2 and Table 1) in the Aire and Calder River valleys, 35 km west of the locality on the Wye River where the species was recorded by Koehn & O'Connor

(1990a). Specimens have been deposited with the Museum of Victoria: NMV A9512 (Calder River); NMV A9513, A9510 (Aire River, drain); NMV A9511 (Aire River, billabong).

Population density of *G. cleaveri* at the three sites could not be estimated because of the dense vegetation and because of the cryptic and nocturnal habits of *G. cleaveri*. The option of clearing aquatic vegetation to sample more effectively was rejected as all sites were small in area.

Associations

All other species associated with *G. cleaveri* (Table 1) are common in the area (Koehn & O'Connor 1990a), are diadromous (with the exception of *Pseudogobius olorum*), and most have been recorded from low-lying swampy habitats. *P. olorum* is usually resident in lower freshwater or estuarine areas as well as in coastal lagoons (Allen 1989), and the specimens of *G. brevipin-*

Site No.	Waterway	Map No. & Grid Ref.	Altitude (m)	Date Sampled	No. Collected	Total Length Range (mm)	Assoc. Species
1	Freshwater Creek[A] (tributary)	8119 493746	20	29.10.80 16.12.80	5 10	37–75[*]	Sfeel,Cgal
2	Wye River[B]	7620 514196	10	14.09.83	1	93[*]	Amm,Cgal,Agrayl, Tup,Btr
3	Calder River (drain)	7620 178056	20	17.10.90	1	90	Sfeel,Cgal
4	Aire River (drain)	7520 147063	10	31.05.90 24.08.90 17.10.90	2 5 2	56–57 74–96 85–90	Sfeel,Cgal Sgal,Bgal,Bsg —
5	Aire R (billabong)	7520 151068	15	16.10.90	1	80	—

amm = lamprey ammocoetes, *Geotria australis* or *Mordacia mordax*
Cgal = common galaxias, *Galaxias maculatus*
Sfeel = short-finned eel, *Anguilla australis*
Sgal = spotted galaxias, *Galaxias truntaceus*
Bgal = broad-finned galaxias, *Galaxias brevipinnis*
Tup = tupong, *Pseudaphritis urvillii*
Btr = brown trout, *Salmo trutta*
Agrayl = Australian grayling, *Prototroctes maraena*
Bsg = blue-spot goby, *Pseudogobius olorum*

[A] from Jackson & Davies (1982)
[B] from Koehn & O'Connor (1990a)
[*] standard lengths

Table 1. Summary of site and collection details for *Galaxias cleaveri* in Victoria.

nis collected were juveniles migrating upstream to adult habitat.

The association of eels and other species of galaxiids with New Zealand mudfish (*Neochanna* spp.) has been observed by Eldon (1968), and *G. cleaveri* has been associated with other galaxiids and with southern pygmy perch, *Nannoperca australis* Günther (Scott 1936, 1971).

In *G. cleaveri* habitats surveyed on mainland Australia the other resident galaxiid species are essentially free-swimming, whereas *G. cleaveri* is benthic. Thus *G. cleaveri* may face natural interspecific competition or predation only from eels which are also benthic and may occupy similar habitats.

Biogeography

The distribution of freshwater native fishes in the Otway region appears to be primarily related to geomorphological conditions that existed during and after the last glaciation 5,000–20,000 years ago (Koehn & O'Connor 1990a). Such conditions restricted non-diadromous freshwater species to the larger Barwon River system to the north and to the Aire and Gellibrand River systems to the south-west, whereas only diadromous species inhabit the short coastal streams.

The diadromous lifecycle of *G. cleaveri* accounts for its occurrence in the Wye River.

Frankenberg (1974) suggested that *G. truttaceus* and *G. brevipinnis*, both species with lifecycles similar to that of *G. cleaveri*, may have migrated to mainland Australia from Tasmania when a land bridge existed during the Pleistocene glaciation. A similar migration may be suggested for *G. cleaveri*. Fulton (1986) described a return to fresh water by juvenile *G. cleaveri* and suggested a marine phase in the species' lifecycle (Fulton 1990). The distribution and residency of the larval phase of *G. cleaveri* is unknown, as is the possibility of land-locked populations of the species not possessing a marine life phase. Such populations are known in other normally diadromous galaxiid species (Pollard 1972, Humphries 1989, Fulton 1990, McDowall 1990).

The present distribution of *G. cleaveri* closely conforms to the region encompassed by the land bridge (Wilsons Promontory to Cape Otway). Larvae developing in marine waters would be dispersed more widely and the species would be expected to be more widely distributed. The occurrence of larval galaxiids as far as 700 km from the coast of New Zealand supports the theory of McDowall (1978) that long-range dispersal of

diadromous species may occur, as is exhibited by *G. truttaceus* and *G. brevipinnis* which are widespread in Victorian coastal streams (Koehn & O'Connor 1990a, 1990c). The more restricted distribution of *G. cleaveri* suggests that the larvae may be confined to estuaries, although further surveys are needed to elucidate dispersal mechanisms.

HABITAT

A comprehensive description of the undisturbed habitat at site 1 was given by Jackson & Davies (1982). Site 2 which is also undisturbed is a small steep stream with a pool–riffle sequence draining mountainous forest country. The substrate consisted of cobbles and gravel, the flow was high, fast and turbid, the conductivity was 150 EC and water temperature was 10°C. It is possible that the specimen found at this site had been washed from areas of low-lying pasture during recent rains.

All new sites were characterised as being modified with all riparian vegetation removed, and sites 3 and 4 had also been channelized.

Site 3 is a shallow channel (1 m wide, 0.2 m deep) with a 0.8 m mud substrate and with water 20–30 mm deep draining from a spring in a pastured paddock into the Calder River. At the time of collection (17 October 1990) the channel had recently been excavated and little vegetation was present. Dissolved oxygen concentrations were 5.7 mg/L, pH was 7.0 and conductivity was 680 EC at 8.0°C. On 27 February 1991 the drain was heavily vegetated with a variety of native and introduced species of aquatic and pasture vegetation, the water was 20–30 mm deep, and the mud substrate was 200–400 mm thick.

Site 4 is a shallow drain (0.2–0.4 m deep) with a silt substrate leading from a spring in a cleared paddock into the Aire River. On 24 August 1990 most of the site consisted of a 2 m wide channel together with a larger 15 m × 20 m area, and was densely vegetated with aquatic species. Conductivity was 185 EC at 10°C. On 17 October 1990 dissolved oxygen concentration was 5.6 mg/L, pH was 6.7, and conductivity was 850 EC at 17°C. On 27 February 1991 there was 100 mm of mud and a little water up to 20 mm deep in cattle hoof prints in the channel. The larger area had shrunk to 3 m × 20 m with up to 100 mm of water and 300 mm of mud. Sections of the drain often become dry during summer but other sections always remain moist due to an underground spring (D. Denney pers. comm.).

Site 5 is a small billabong (60 m × 5 m × 0.8 m deep) about 30 m from the Aire River. No flow was apparent and the substrate was silt with dense aquatic vegetation. On 16 October 1990 the water was dark tannin in colour and had a dissolved oxygen concentration of 4.0 mg/L, pH of 6.4 and conductivity of 190 EC at 16.5°C. One specimen of *G. cleaveri* was collected from just inside a large log lying in the water. On 27 February 1991 the site was completely dry, a condition not unusual for this season (D. Denney pers. comm.).

All sites are at low altitudes (a maximum of 20 m above sea level) and close to the sea (a maximum of 8.5 km from the sea but only 3 km from brackish water). Except for site 2, all sites had no discernible flow and had mud or silt substrates and dense aquatic vegetation. Although Andrews (1976) considered that *G. cleaveri* tolerated brackish water, all our specimens were collected from fresh water. The drain leading from site 3, however, flowed into reaches of the Aire River which are known regularly to contain an estuarine salt-wedge under low flow conditions (J. Koehn pers. obs.).

The presence of *G. cleaveri* at these sites is consistent with its occurrence elsewhere in swamps, drains and semi-permanent waters. *G. cleaveri* was collected from stagnant pools in Tasmania (Andrews 1976) and from a drainage system usually dry in summer on Flinders Island (Green 1984). Fulton (1986) also recorded *G. cleaveri* from a dry section of the Esperance River in Tasmania. In New Zealand three species of mudfish, *Neochanna burrowsius, N. apoda* and *N. diversus*, have also been described as specialised to life in swamps, creeks and drains that tend to dry up in summer (Eldon 1968, 1978, 1979a, McDowall 1990).

Scott (1934) described *G. cleaveri* as one of the most specialised galaxiids in having adopted a mode of life suited to such habitats. Such adaptation and an association with low altitude, swampy habitats is likely to indicate a high degree of dependance on the presence of appropriate habitats. Collection of the species in Victoria from disjunct and highly modified areas containing introduced vegetation suggests that these populations may be remnants of a larger population that once existed when suitable habitats were more widespread.

BEHAVIOUR

We kept four *G. cleaveri* from site 3 in a glass aquarium (0.36 × 0.45 × 0.10 m) containing a silt

substrate and vegetation from the site. The behaviour and position of the fish were observed at intervals throughout each day for three weeks, and at 5 minute intervals for 1 hour during one night.

Generally the fish were inactive during the day, resting either on the substrate or amongst vegetation, and were difficult to locate because of their colour and cryptic habit. Individuals spent time resting either on the substrate wherever cover was available, or amongst dense weed just below the water surface. In both situations, several individuals shared the same cover and were in physical contact with each other. This behaviour is similar to that described by Eldon (1969) in *Neochanna apoda* which is also territorial and aggressive to other species in aquaria (Eldon 1968). Individuals of *G. cleaveri* exhibited no such aggressive behaviour to each other or to individuals of *Galaxias maculatus* or *G. truttaceus* which were placed into the aquaria at different times. At night *G. cleaveri* were more active, continually moving around open areas "browsing". At least two of the fish were in open areas at each observation. They immediately retreated into the vegetation when exposed to either white or red light but had always reappeared in the unvegetated areas by the next observation.

Our observations indicate that *G. cleaveri* is a nocturnal, cryptic species which often inhabits the aquatic vegetation rather than the substrate. Other species of galaxiids reported to be nocturnal are *Neochanna apoda* (Eldon 1968), *Galaxias brevipinnis* (Glova & Sagar 1989a), and *Galaxias vulgaris* Stokell (Glova & Sagar 1989b).

AESTIVATION

Scott (1934) gave details of the ability of *G. cleaveri* to aestivate, though under unnatural conditions. This ability has been noted by several other authors (Fletcher 1907, Hall 1901, Fulton 1986) though their descriptions mainly concern recovery of aestivating individuals. Fulton (1986) provided photographic evidence of *G. cleaveri* aestivating during mid-summer under a rock at least 10 m from free water.

McDowall & Pusey (1983) reported aestivation in *Lepidogalaxias salamandroides*, and aestivation of *Galaxiella pusilla* was suggested by McDowall & Frankenberg (1981). Humphries (1985) tested this suggestion by maintaining specimens of *G. pusilla* in an aquarium for 36 days whilst lowering water levels and maintaining oxygen concentrations at less than 5 ppm. Fish survived on the surface of the mud and in a small hole for several days in the absence of surface water. McDowall (1990) presented evidence of the ability of the New Zealand mudfishes *Neochanna burrowsius* and *N. apoda* to survive dry periods, though both Eldon (1978) and Meredith (1985) concluded that these species do not exhibit true aestivation during which the individual becomes torpid and the normal rate of metabolism decreases.

We investigated whether burrowing and aestivation could be induced in *G. cleaveri* by placing two individuals (101 mm and 78 mm TL) into a glass aquarium ($0.3 \times 0.62 \times 0.3$ m) containing a substrate of soil and mud, a large flat rock at one end, dense aquatic vegetation in the middle, and a piece of log at the other end. The water level was lowered artificially, and heating and illumination were provided during the day by an incandescent globe. On day 10 some tunnelling in the middle section of the tank was observed, and one fish was seen lying near the water surface where it spasmodically gulped water and air. On day 14, when the water level had fallen to 10 mm above the substrate, one fish was resting in a vertical shaft in the mud with its head just protruding. On day 22 neither fish could be seen and no surface water remained, though water was present in the opening of the shaft. Later on the same day the heads of both fish were positioned in the shaft opening and their bodies were under the mud in horizontal tunnels. On day 25 a series of smaller openings were observed in a line directed away from the large shaft, presumably along the horizontal tunnels. On day 31 there was no water in the pit of the large shaft, the mud substrate had begun to dry, and one *G. cleaveri* had its head protruding from the tunnel into the shaft below the surface of the substrate. On day 32, after 5 days without any free water, the fish in the tunnels stopped moving. On day 42 when the substrate had dried to only 30 mm thick the two *G. cleaveri* were seen through cracks in the dry mud lying in the tunnels. The tank was then slowly rehydrated, and the fish recovered movement and emerged when the mud became soft. They both immediately fed on earthworms and showed no ill effects from surviving in stagnant water for 14 days and without surface water for another 14 days.

Whilst not physiologically confirming the ability of *G. cleaveri* to aestivate, our study shows that the species can survive periods without free surface water by burrowing into the substrate.

LIFECYCLE

Two male *G. cleaveri* collected at site 4 on 31 May 1990 were in a ripe spawning stage (Pollard 1972), whereas individuals collected on 24 August 1990 were all spent or undeveloped, indicating a winter spawning. These observations are consistent with those of Andrews (1976) who reported fully developed eggs in a specimen of *G. cleaveri* examined in Tasmania during May. After ageing whitebait returning to freshwater as approximately 2 months old, Fulton (1986) suggested that *G. cleaveri* spawn during mid-winter, and he believes (W. Fulton pers. comm.) that juvenile *G. cleaveri* return to fresh water during spring along with other galaxiids.

Cadwallader (1975) and Eldon (1979a) concluded that *Neochanna burrowsius* in New Zealand spawns during late winter and early spring in habitats frequented by adults. In contrast, Eldon (1979a) suggested that *N. apoda* spawns during most months of the year, especially when a drought breaks. Because Eldon (1971) found that in an aquarium *N. apoda* deposited eggs above the waterline, he speculated that in the wild the species deposits eggs out of the water amongst damp vegetation and detritus. The spawning location of *G. cleaveri* has not yet been found.

Present evidence indicates that *G. cleaveri* is unique amongst galaxiids in possessing the two characteristics of aestivation and diadromy.

THREATS AND CONSERVATION STATUS

General threats to freshwater native fish in Victoria have been described by Koehn & O'Connor (1990b) who considered habitat removal and alteration a prime reason for the decline of many species. The reliance of *G. cleaveri* on specific habitat would appear to make it susceptible to habitat changes, particularly the loss of wetland habitat.

The maintenance of fish habitats has been recognised as a key issue in management of the State's freshwater fish fauna (Koehn & O'Connor 1990c). Whilst up to one-third of the State's wetlands have been destroyed (DCE 1988), most of the assessments have related only to waterbirds; further assessments in relation to changes to fish habitats are necessary. Corrick (1981, 1982) and Corrick & Norman (1980) assessed coastal wetlands in southern Victoria and assigned them to the following categories.

1. Flooded river flats: land inundated for very short periods following rain or flooding.

2. Freshwater meadows: land with waterlogged soil for up to 3 months each year but where surface water is shallow and transient.
3. Shallow freshwater marshes: land with waterlogged soil throughout the year, and where surface water may be present for 6 to 9 months.
4. Deep freshwater marshes: land inundated to a depth of more than 1 m during years of average or above average rainfall.
5. Permanent open fresh water: water storages and natural lakes deeper than 1 m.
6. Semi-permanent saline wetlands.
7. Permanent saline wetlands.

From our knowledge of the habitats of adult *G. cleaveri*, shallow freshwater marshes (category 3) and deep freshwater marshes (category 4) appear to provide permanent areas of habitat. Flooded river flats and freshwater meadows may be used temporarily by the species during migration of whitebait or migration of adults to estuarine areas. Open fresh water (category 5) is unlikely to be used, particularly if lacking vegetation. There is no evidence to suggest that saline wetlands (categories 6 and 7) provide suitable habitats.

In a study of the Snowy River and Gippsland Lakes catchments, Corrick & Norman (1980) concluded that 25% of shallow and 34% of deep freshwater marshes have been lost. Within the Port Phillip Bay region, valuable wetlands lost include the Edithvale–Carrum–Seaford Swamps (Champion 1977, Donnelly et al. 1985) and the swamps of the lower Yarra and Maribyrnong Rivers (Castelnau 1872, excerpts from a diary kept by J. Flemings reprinted in Shillinglaw 1879, Kenyon 1934, and Ducker 1985). After studying wetlands between Port Phillip Bay and Mt Emu Creek in western Victoria, Corrick (1982) concluded that 79% of shallow and 66% of deep freshwater marshes had been lost since European settlement, an overall loss of 73% of potential *G. cleaveri* habitat. The most extensive habitat loss, however, is in South Gippsland where 95% of the natural freshwater wetland once present has been destroyed (Corrick 1981). South Gippsland also includes the largest areas of potential *G. cleaveri* habitat because it contains coastal-draining wetlands only within 40 km of the coast, unlike the other areas where wetlands extend as far as 150 km inland.

More than 23,000 ha of wetlands have been lost in South Gippsland, including Koo-Wee-Rup, Cardinia and Yallock Swamps, and swamps along the Powlett and Tarwin Rivers.

Corrick (1981) predicted further loss of wetland areas through drainage, clearing, cultivation and flood mitigation and irrigation works. His prediction appears fulfilled because calculations from recent studies of this area (Corrick unpubl. data) show an overall loss of 99% of potential *G. cleaveri* habitat (shallow freshwater marshes 94%, deep freshwater marshes 99%).

The loss of such large areas of habitat suitable for *G. cleaveri* must be the greatest threat to this species in Victoria in recent times and may account for its fragmented distribution. Similarily, Frankenberg (1974) stated that the range of *G. cleaveri* in Tasmania had undoubtedly been fragmented due to the draining and clearing of swamps.

In New Zealand populations of the three species of mudfish have declined drastically with the loss of habitat due to swamp drainage, development and agricultural practices (McDowall 1990). Whilst concern has been expressed for all three species, Skrzynski (1968) and Eldon (1979b) have questioned whether *Neochanna burrowsius* can survive, especially with continued agricultural modifications. Cadwallader (1975) suggested that preservation of habitat areas through the establishment of reserves should be instigated for this species. A population of *N. burrowsius* established in an artificial pond (Eldon 1988) survived for several years before dying out as a result of a prolonged drought (NZ MAF 1990)

Other threats to adult *G. cleaveri*, such as interspecific competition and predation by introduced trout, *Salmo trutta*, *Oncorhynchus mykiis* or redfin, *Perca fluvialitis*, are unlikely to be major, especially in swampy habitats with poor water quality unsuitable to these species. *G. cleaveri* whitebait may be subject to predation, however, whilst migrating upstream. Habitat disturbance and competition from other introduced species such as carp, *Cyprinus carpio*, goldfish, *Carassius auratus*, and tench, *Tinca tinca*, are possible but difficult to assess. Sedimentation is unlikely to affect *G. cleaveri* unless the habitat areas become completely filled.

Because *G. cleaveri* is restricted to a specialised aquatic habitat, climatic changes may have serious impacts, although the impact of the Greenhouse Effect is as difficult to predict as it is for other native species (Burchmore 1990). Lower winter rainfall may affect spawning and particularly access to the sea, and an increase in the tidal limit may alter available wetland habitat for mature *G. cleaveri*.

In a recent review of the conservation status of native fish in Victoria (Koehn & Morison 1990) *G. cleaveri* was listed as vulnerable, a category including "taxa not presently endangered but which are at risk by having small populations and/or by occupying restricted habitats susceptible to rapid environmental change and/or populations which are declining at a rate that would render them endangered in the near future". Although we have documented additional localities for *G. cleaveri*, our results reinforce the rarity of the species. The reductions in available freshwater wetlands and ongoing threats to such habitats justify the retention of *G. cleaveri* in the vulnerable category.

CONCLUSIONS

G. cleaveri is more widespread in Victoria than previously believed, occupying natural and modified habitats along lowland coastal areas, at least from Wilsons Promontory to the western Otways. There is a need for further surveys to determine the range of the species in swampy habitats within and outside of this area, particularly on French Island which contains remnant tea-tree swamp habitat that once existed throughout the Koo-Wee-Rup swamp area and the entire Western Port catchment. The discovery of *G. cleaveri* in this area would strengthen arguments that present populations are remnants of a once much larger, more uniformly distributed population. Collection of whitebait as they ascend coastal streams may also be a useful method of determining *G. cleaveri* distribution (Koehn & O'Connor 1990a).

The behaviour and habitat needs of this species are similar to those of the New Zealand mudfishes. The specific habitat needs of *G. cleaveri* make it particularly susceptible to habitat changes; therefore the massive reductions in suitable freshwater wetland habitats have undoubtedly been the greatest threat to the species. The management and conservation of such wetland areas are vital for the preservation of *G. cleaveri* in Victoria.

ACKNOWLEDGEMENTS

Winch and Irene Prentice. This work was completed as part of the Silviculture Systems Project funded by the Department of Conservation and Environment, Victoria.

REFERENCES

ALLEN, G. R., 1989. *Freshwater Fishes of Australia.* TFH Publications, USA.

ANDREWS, P. A., 1976. A revision of the family Galaxiidae (Pisces) in Tasmania. *Australian Journal of Marine and Freshwater Research* 27: 297–349.

BACKHOUSE, G. N. & VANNER, R. W., 1978. Observations on the biology of the dwarf galaxiid, *Galaxiella pusilla* (Mack) (Pisces: Galaxiidae). *Victorian Naturalist* 95: 128–132.

BECK, R. G., 1985. Field observations upon the dwarf galaxiid *Galaxiella pusilla* (Mack) (Pisces: Galaxiidae) in the south-east of South Australia. *South Australian Naturalist* 60: 12–22.

BURCHMORE, J. J., 1990. Implications of the greenhouse effect for native freshwater fishes in New South Wales. *Wetlands* 10 (1/2): 30–32.

CADWALLADER, P. L., 1975. Distribution and ecology of the Canterbury mudfish, *Neochanna burrowsius* (Phillipps) (Salmoniformes: Galaxiidae). *Journal of the Royal Society of New Zealand* 5: 21–30.

CADWALLADER, P. L. & BACKHOUSE, G. N., 1983. *A Guide to the Freshwater Fish of Victoria.* Victorian Government Printer, Melbourne, 249 p.

CASTELNAU, F. L. DE, 1872. Contributions to the ichthyology of Australia. *Proceedings of the Zoological and Acclimatisation Society of Victoria* 1: 29–242.

CHAMPION, R., 1977. Edithvale–Carrum–Seaford wetlands. Graeme Shaw, Denton and Corker & Randall Champion–Conservation Planning, Melbourne.

CORRICK, A. H., 1981. Wetlands of Victoria 2. Wetlands and waterbirds of South Gippsland. *Proceedings of the Royal Society of Victoria* 92: 187–200.

CORRICK, A. H., 1982. Wetlands of Victoria 3. Wetlands and waterbirds between Port Phillip Bay and Mount Emu Creek. *Proceedings of the Royal Society of Victoria* 94: 69–87.

CORRICK, A. H. & NORMAN, F. I., 1980. Wetlands of Victoria 1. Wetlands of the Snowy River and Gippsland Lakes catchment. *Proceedings of the Royal Society of Victoria* 91: 1–15.

DCE (DEPARTMENT OF CONSERVATION & ENVIRONMENT), 1988. *Wetlands Conservation Program for Victoria.* Victorian Government Printer, Melbourne.

DONNELLY, A., KUNERT, C. & SCHLEIGER, P., 1985. Ecology and management of Seaford Swamp. A study of a remnant wetland on the rural fringe of metropolitan Melbourne. Graduate School of Environmental Science, Monash University, Environmental Report No. 25.

DUCKER, S. C., 1985. James Fleming: the first gardener on the River Yarra, Victoria. *Archives of Natural History* 13: 123–140.

ELDON, G. A., 1968. Notes on the presence of the brown mudfish (*Neochanna apoda* Günther) on the west coast of the South Island of New Zealand. *New Zealand Journal of Marine and Freshwater Research* 2: 37–48.

ELDON, G. A., 1969. Observations on growth and behaviour of Galaxiidae in aquariums. *Tuatara* 17: 34–46.

ELDON, G. A., 1971. Suspected terrestrial deposition of eggs by *Neochanna apoda* Günther (Pisces: Salmoniformes: Galaxiidae). *Journal of Fish Biology* 3: 247–249.

ELDON, G. A., 1978. The life history of *Neochanna apoda* Günther (Pisces: Galaxiidae). *New Zealand Ministry of Agriculture and Fisheries, Fisheries Research Bulletin* 19: 1–44.

ELDON, G. A., 1979a. Breeding, growth and aestivation of the Canterbury mudfish, *Neochanna burrowsius* (Salmoniformes: Galaxiidae). *New Zealand Journal of Marine and Freshwater Research* 13: 331–346.

ELDON, G. A., 1979b. Can the Canterbury mudfish survive? *Catch* (NZ) 6: 19.

ELDON, T., 1988. Canterbury mudfish established in a new pond. *Freshwater Catch* 36: 5.

FLETCHER, H. J., 1907. Notes and exhibits. *Proceedings of the Linnaean Society of New South Wales* 31: 430–431.

FRANKENBERG, R. S., 1967. The vertebrate fauna of the Bass Strait Islands. The galaxiid fishes of Flinders and King Islands. *Proceedings of the Royal Society of Victoria* 80: 225–228.

FRANKENBERG, R. S., 1974. Native freshwater fish. In *Biogeography and Ecology in Tasmania* (Monographiae Biologicae 25), W. D. Williams, ed., W. Junk, The Hague, 113–140.

FULTON, W., 1986. The Tasmanian mudfish *Galaxias cleaveri*. *Fishes of Sahul* 4: 150–151.

FULTON, W., 1990. *Tasmanian Freshwater Fishes.* Fauna of Tasmania Handbook No. 7, Fauna of Tasmania Committee, Hobart.

GLOVA, G. J. & SAGAR, P. M., 1989a. Feeding in a nocturnally active fish, *Galaxias brevipinnis*, in a New Zealand stream. *Australian Journal of Marine and Freshwater Research* 40: 231–40.

GLOVA, G. J. & SAGAR, P. M., 1989b. Prey selection by *Galaxias vulgaris* in the Hawkins River, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 25: 153–161.

GREEN, R. H., 1984. The Tasmanian mudfish on Flinders Island. *Tasmanian Naturalist* 77: 7.

HALL, T. S., 1901. A burrowing fish (*Galaxias* sp.). *Victorian Naturalist* 18: 65–66.

HUMPHRIES, P. L., 1985. Aspects of biology of the dwarf galaxiid, *Galaxiella pusilla* (Mack) (Salmoniformes: Galaxiidae). BSc (Hons) thesis, Monash University, Clayton, Victoria.

HUMPHRIES, P. L., 1986. Observations on the ecology of *Galaxiella pusilla* (Mack) (Salmoniformes: Galaxiidae) in Diamond Creek, Victoria. *Proceedings of the Royal Society of Victoria* 98: 133–137.

HUMPHRIES, P. L., 1989. Variation in the life history of diadromous and landlocked populations of the spotted galaxias, *Galaxias truttaceus* Valenciennes, in Tasmania. *Australian Journal of Marine and Freshwater Research* 40: 501–518.

JACKSON, P. D. & DAVIES, J.N., 1982. Occurrence of the Tasmanian mudfish, *Galaxias cleaveri* Scott, on Wilsons Promontory: first record from mainland Australia. *Proceedings of the Royal Society of Victoria* 94: 49–52.

KENYON, A. S., 1934. *Heidelberg, the City of Streams.* City of Heidelberg Centenary Celebrations Committee.

KOEHN, J. D., 1990. *A Bibliography of Research Publications by Staff of the Freshwater Fish Management Branch, Fisheries Division, 1970–90.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 102, Department of Conservation, Forests and Lands, Victoria.

KOEHN, J. D. & MORISON, A. K., 1990. A review of the conservation status of native freshwater fish in Victoria. *Victorian Naturalist* 107: 13–25.

KOEHN, J. D. & O'CONNOR, W. G., 1990a. The distribution of freshwater fish in the Otway Region, south-western Victoria. *Proceedings of the Royal Society of Victoria* 102: 29–39.

KOEHN, J. D. & O'CONNOR, W. G., 1990b. Threats to Victorian native freshwater fish. *Victorian Naturalist* 107: 5–12.

KOEHN, J. D. & O'CONNOR, W. G., 1990c. *Biological Information for Management of Native Freshwater Fish in Victoria.* Government Printer, Melbourne, 165 p.

KOEHN, J. D., McKENZIE, J. A., O'CONNOR, J. P., O'CONNOR, W. G., O'MAHONY, D. J., RAADIK, T. A., SADDLIER, S. R. & TUNBRIDGE, B. R., 1991. *Miscellaneous Surveys of Freshwater Fish in Victoria.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 110, Department of Conservation and Environment, Victoria.

McDOWALL, R. M., 1978. Generalised tracks and dispersal in biogeography. *Systematic Zoology* 27: 88–104.

McDOWALL, R. M., 1990. *New Zealand Freshwater Fishes. A Natural History and Guide.* Heinemann Reed, Auckland, New Zealand, 553 p.

McDOWALL, R. M. & FRANKENBERG, R. S., 1981. The galaxiid fishes of Australia. *Records of the Australian Museum* 33: 443–605.

McDOWALL, R. M. & PUSEY, B. J., 1983. *Lepidogalaxias salamandroides* Mees – a redescription, with natural history notes. *Records of the Western Australian Museum* 11: 11–23.

McDOWALL, R. M. & WHITAKER, A. M., 1975. The freshwater fishes. In *Biogeography and Ecology in New Zealand (Monographiae Biologicae 27)*, G. Kuschel, ed., W. Junk, The Hague, 277–299.

MEREDITH, A. S., 1985. Metabolism and cutaneous exchange in an amphibious fish, *Neochanna burrowsius* (Phillipps). PhD thesis, University of Canterbury, Christchurch.

NZ MAF (NEW ZEALAND MINISTRY OF AGRICULTURE AND FISHERIES), 1990. *Freshwater Fisheries Centre Annual Report, 1989.* MAF, Wellington, New Zealand.

POLLARD, D. A., 1972. The biology of a landlocked form of the normally catadromous salmoniform fish *Galaxias maculatus* (Jenyns). 3. Structure of gonads. *Australian Journal of Marine and Freshwater Research* 23: 17–38.

SCOTT, E. O. G., 1934. Observations on some Tasmanian fishes, with descriptions of new species. *Papers and Proceedings of the Royal Society of Tasmania* (1933): 31–53.

SCOTT, E. O. G., 1936. Observations on fishes of the family Galaxiidae. Part 1. *Papers and Proceedings of the Royal Society of Tasmania* (1935): 85–112.

SCOTT, E. O. G., 1971. On the occurrence in Tasmania and on Flinders Island of *Brachygalaxias* Eigenmann, 1928 (Pisces: Galaxiidae) with description of two new species. *Records of the Queen Victoria Museum Launceston* 37: 1–14.

SHILLINGLAW, J. J., 1879. *Historical Records of Port Phillip Bay.* Victorian Government Printer, Melbourne.

SKRZYNSKI, W., 1968. The Canterbury mudfish, *Galaxias burrowsius* Phillipps, a vanishing species. *New Zealand Journal of Marine and Freshwater Research* 2: 688–97.

THOMPSON, F. V., 1987. Notes on the biology of the black mudfish. *Freshwater Catch* 32: 6–10.

FIRST RECORDS OF *MIRACYTHERE* HORNIBROOK, 1952 (CRUSTACEA, OSTRACODA) FROM THE TERTIARY OF AUSTRALIA

J. V. Neil

Department of Geology, University of Melbourne, Parkville, Victoria 3052
Present address: 23 Michael Street, Bendigo, Victoria 3550

A new species of the rare ostracode genus *Miracythere* Hornibrook, 1952, previously known only from New Zealand, is described from late Early or early Middle Miocene (Batesfordian) strata of the Muddy Creek Formation near Hamilton, southwestern Victoria. The new species is not formally named because the only complete adult valve amongst the limited material discovered has been lost. A specimen of another undescribed species possibly belonging to *Miracythere* is also figured from the Late Eocene of South Australia. The literature relating to this genus is reviewed, and the morphological parallels between *Miracythere* and some Palaeozoic genera are briefly discussed.

MIRACYTHERE is a rare and distinctive ostracode genus erected by Hornibrook (1952) for his new species *M. novaspecta* from dredgings off the northern tip of New Zealand. He indicated that the type species is widely distributed in New Zealand waters, though no locality data were given. No other species of the genus has been described, and the only other documented occurrence of *M. novaspecta* has been two valves recorded from the Otago Shelf by Swanson (1979a).

Hornibrook (1952, 1968) gave the stratigraphic range of *Miracythere* as Late Eocene (Runangan) to Recent and of *M. novaspecta* as Early Miocene (Hutchinsonian) to Recent, but he did not record any fossil occurrences. He has recently informed me (written communication 1985) that the Eocene occurrence cannot be confirmed, but that a specimen of *M. novaspecta* is known from the Wharekuri Greensand of Late Oligocene (Duntroonian) age, at a locality on the Waitaki River in the South Island now submerged by a hydroelectricity scheme reservoir. That occurrence, and a broken specimen (Fig. 1B) of ?*Miracythere* that I have recovered from the Tuketja Member of the Blanche Point Formation of South Australia (Late Eocene; Jenkins et al. 1982), predate the Victorian species described in the present paper. I have also picked a specimen of another undescribed species of ?*Miracythere* from a sample supplied by Dr B. Hayward from the Pleistocene (Castlecliffian Stage) Wanganui Series of New Zealand (Fig. 2C). No other occurrences of the genus are known at present.

SYSTEMATIC PALAEONTOLOGY

Family BYTHOCYTHERIDAE Sars, 1866

Remarks. Hornibrook (1952) placed *Miracythere* in the Bythocytherinae but noted that the hinge, with a posterior tooth in the left valve, is more complex than the characteristic bythocytherinid hinge. Schornikov (1981) regarded the genus as Bythocytherinae *incertae sedis*. Since I follow Hartmann & Puri (1974) in not recognising subfamilial groupings within the Bythocytheridae, the question of the placement of *Miracythere* at the subfamilial level does not arise. The hinge type as diagnosed by Hornibrook, and its variation in the Victorian species described here, fall within the range accepted as "normal" for bythocytherids.

Genus Miracythere Hornibrook, 1952

Type species. Miracythere novaspecta Hornibrook, 1952.

Diagnosis. See Hornibrook 1952: 61–62.

Remarks. A specimen from the Gulf of California and another of Cretaceous age from a deep sea drilling core in the Shatsky Rise, northwestern Pacific Ocean (DSDP 6-48.2) were tentatively assigned to *Miracythere* by Swain (1967; in Maddocks 1983). Both specimens differ from *M. novaspecta* in lacking a median sulcus, being longer, being caudate rather than subquadrate, and in having reticulate rather than smooth-surfaced valves. These differences

suggest that the specimens do not belong to *Miracythere*.

Miracythere sp. A

Figs 1A, C–D, 2A–B, 3A, C–F

Material. The specimens originally found consisted of one adult left valve (Figs 1A, D, 2A–B, 3A, C–F), one juvenile left valve, and fragments of two valves, all of which were lost in transit to the laboratory of the Geological Survey of Victoria. Subsequent repicking of the sample produced two broken juvenile valves, one left (NMV P123311, Fig. 1C) and one right (NMV P123312). The catalogue numbers refer to the invertebrate palaeontological collection of the Museum of Victoria, Melbourne.

Horizon and locality. Muddy Creek Formation, Clifton Bank, Muddy Creek near Hamilton, southwestern Victoria.

Age. All the specimens came from the oldest level at Clifton Bank (Sample 9), of late Early or early Middle Miocene (Batesfordian) age (N8 in the planktonic foraminiferal zones of Berggren et al. 1985; the revised correlation of magnetic anomalies by Berggren et al. has shifted ages 1.5 to 2.0 my younger in the Middle Miocene, so that the position of the Early–Middle Miocene boundary in relation to the Australian Bairnsdalian and Balcombian stages is open to debate.)

Dimensions. Adult LV: L = 0.65 mm; H = 0.38 mm; W = 0.23 mm (figured specimen, now lost). The repicked specimens NMV P123311 and P 123312 are too fragmentary to measure.

Description. Valve medium-sized in adult; subelliptical in outline, hyaline and thinly calcified. Surface smooth. Normal pore canals simple and widely scattered. Dorsal margin straight. Ventral margin straight to slightly sinuous, subparallel to dorsal margin except posteriorly. Anterior and posterior gently rounded in outline, former more so than latter. Anterodorsal and posterodorsal angles broadly and evenly rounded. Shallow, vertical median sulcus. Prominent hollow tubercle developed anterodorsally (Figs 1A, 3A), ornamented with three spines on dorsal edge. Valve inflated, with well-developed and sharply-defined flattened ventral zone; less marked flattening anteriorly and posteriorly. Inflation of valve greatest in posterior third. Marginal zone of valve and inflated area ornamented with flat spatulate spines (Fig. 3E) that vary in orientation, from normal to plane of valve dorsally, to parallel with that plane ventrally. Ends of spines trilobate, bilobate or pointed (Figs 3E, F). Spines absent along dorsal margin. Ventrally, spines separated from basal

plane of valve by slightly flanged rim. Approximately 30 spines in one row around inflated portion of carapace. Some spines probably missing through damage to valve. Spines 2 or 3 times more numerous on juvenile specimens than on adult. Ventral marginal zone of inflated area flat and normal to valve plane, forming broad basal platform 0.2 mm across (single valve).

Hinge-line marked in left valve by simple, smooth median bar with long, narrow grooves at anterodorsal and posterodorsal angles (Figs 2B, 3C, D). Muscle scar pattern consisting of 5 adductors in a compressed vertical row, with 2 small, subcircular frontal scars, one small ventral mandibular scar and 2 prominent dorsal scars (Fig. 2A). Inner margin moderately broad in anterior, narrow in posterior (Fig. 1D). Radial pore canals not detected. Line of concrescence deviates from inner margin; vestibule moderately broad anteriorly, narrow posteriorly. No eye tubercle. Sexual dimorphism not known.

Affinities. Miracythere sp. A differs from *M. novaspecta* (Figs 1E, 3B) in its more rounded ends and its spatulate rather than "peg-like" spines which occur in a single row marginal to the valve and the inflated area, rather than in 2 or 3 rows. The tubercle of the present species also carries spines rather than the pustules found on *M. novaspecta* (Fig. 3B). Additionally, there is no tooth in the hinge elements of the left valve. *Miracythere* sp. A resembles the type species in the median vertical sulcus, the ornamentation of spines, the muscle scar pattern and the shape and appearance of the carapace in lateral view. These features clearly establish the species as belonging to *Miracythere*.

Remarks. Miracythere sp. A is more closely allied morphologically to the Pleistocene specimen from New Zealand (Fig. 2C) than it is to *M. novaspecta* (Fig. 1E), having a similar arrangement of spines, a lophodont hinge structure and a similar subrounded quadrate shape. However, the Pleistocene specimen does not have a clearly differentiated, inflated inner lateral section of the valve as found in *Miracythere* sp. A. The fragmentary valve from the Late Eocene of the Blanche Point Formation, South Australia (Fig. 1B) may be conspecific with *Miracythere* sp. A.

The dimensions of the lost adult specimen of *Miracythere* sp. A were the same as those of the holotype *M. novaspecta*, allowing for the fact that the former specimen was a single valve whereas the latter is a carapace. It was not possible to determine whether this adult valve be-
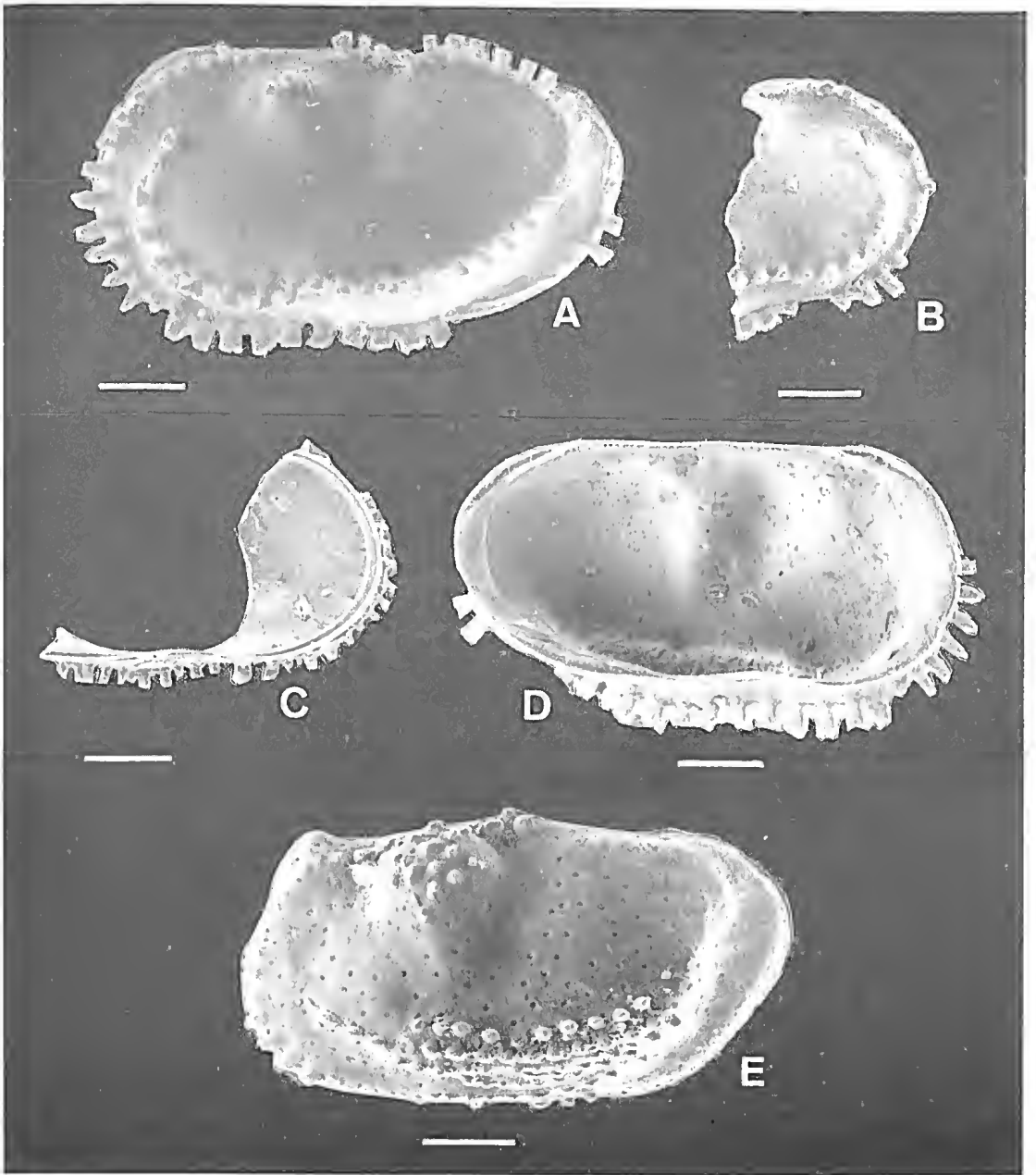
Fig. 1. A, C, D, *Miracythere* sp. A, Muddy Creek Marl (early Middle Miocene), Clifton Bank, Muddy Creek, southwestern Victoria. A, D, LV exterior and interior (specimen lost). C, LV interior (fragmentary juvenile), NMV P123311. B, ?*Miracythere* sp., LV exterior (fragment), Tuketja Member, Blanche Point Formation (Late Eocene), Port Willunga, South Australia. E, *Miracythere novaspecta* Hornibrook, 1952, LV exterior, New Zealand Geological Survey fossil locality F201012, Station 18 of Hornibrook (1952), off Big King Island at 98 fathoms. Scale bars = 0.1 mm.
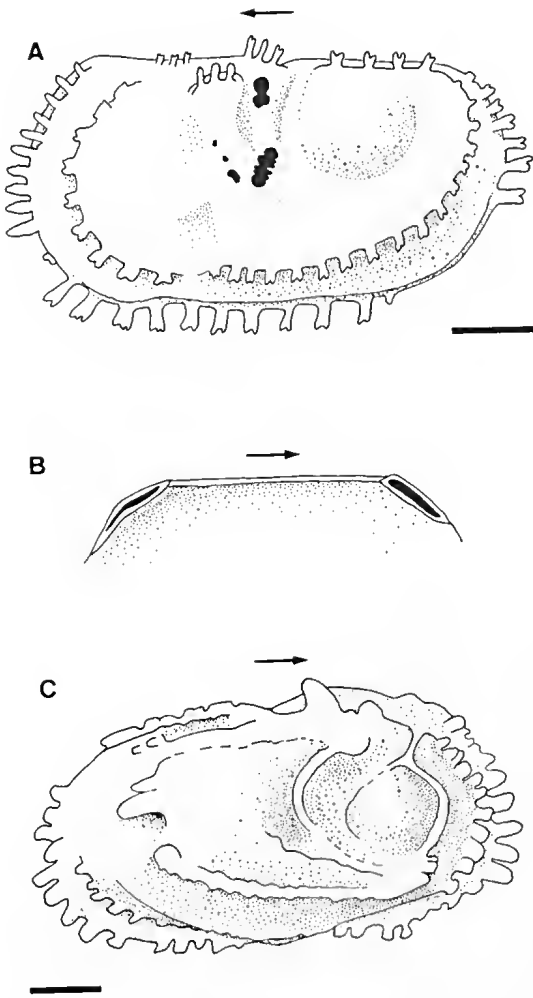
Fig. 2. A–B, *Miracythere* sp. A. A, drawing of LV interior showing muscle scars. B, drawing of LV hinge line (not to scale). C, *?Miracythere* sp., drawing of RV exterior, from Wanganui Series (Castlecliffian, Pleistocene), Wanganui, New Zealand. Scale bars = 0.1 mm.

longed to a male or to a female. The juvenile specimen (now lost) was close to the adult in lateral dimensions but was much less inflated, suggesting that in the final growth stage or stages there was little change in length or height but an increase in width. However, Swanson (1979a) figured a specimen of *M. novaspecta* that he considered to be a juvenile, though its length and height are virtually the same as those of the holotype and its width is actually greater.

The hinge structure of *Miracythere* sp. A is closer to the typical bythocytherid form than to that of the type species. In the latter, the left valve anterior groove or socket of the hinge elements extends above the dorsal line established by the median bar, and marks the anterodorsal angle in pronounced fashion (Fig. 3D). *Miracythere* sp. A has a narrow anterior groove which continues the line of the median bar, paralleling the broadly rounded anterodorsal angle (Fig. 3C). The left valve posterior hinge element of *M. novaspecta* consists of a narrow tooth below, with a groove or socket above at the posterodorsal angle. *Miracythere* sp. A has a groove (in a more elongate form), no tooth and a less marked posterodorsal angle (Fig. 3C). The Victorian and Late Eocene South Australian specimens have a lophodont hinge structure. Given that the variation in hinge structure is a relatively minor one, the specimens should be retained in *Miracythere*.

As with the genera *Puncia* and *Manawa* erected by Hornibrook (1949), morphological parallels may be drawn between *Miracythere* and some Palaeozoic genera. Ruggieri & Siveter (1975) figured a species of *Kelletina*, *K. carnica*, in which there is ventrally a broad flat platform or flange with marginal spines, some of which are linked to form a perforated ridge. *Kelletina carnica* also has a lophodont hinge structure very similar to that of *Miracythere* sp. A. The right valve of *K. carnica* has a simple tooth at each of the anterodorsal and posterodorsal angles to match the grooves in the left valve. The unknown right valve of *Miracythere* sp. A is likely also to have such teeth. A further similarity with Palaeozoic genera lies in the muscle scar pattern, which in both *Miracythere* and *Promanawa* McKenzie & Neil, 1983 includes prominent dorsal antennal/mandibular scars.

Morphological similarities with Palaeozoic forms gave rise to speculation about the phylogeny of the Punciidae by Hornibrook (1949, 1963), even though at that time no Mesozoic representatives of the family were known. Herrig (1988), however, has recently discovered species of all three punciid genera, *Puncia*, *Manawa* and *Promanawa*, in silicified chalky limestone of late Maastrichtian age. Swanson (1991) made an intensive study of the soft part anatomy of punciids, as well as their carapace morphology, and concluded that "On the basis of a detailed comparison of a number of key carapace characters ... punciid ostracods are the only living representatives of the predominantly
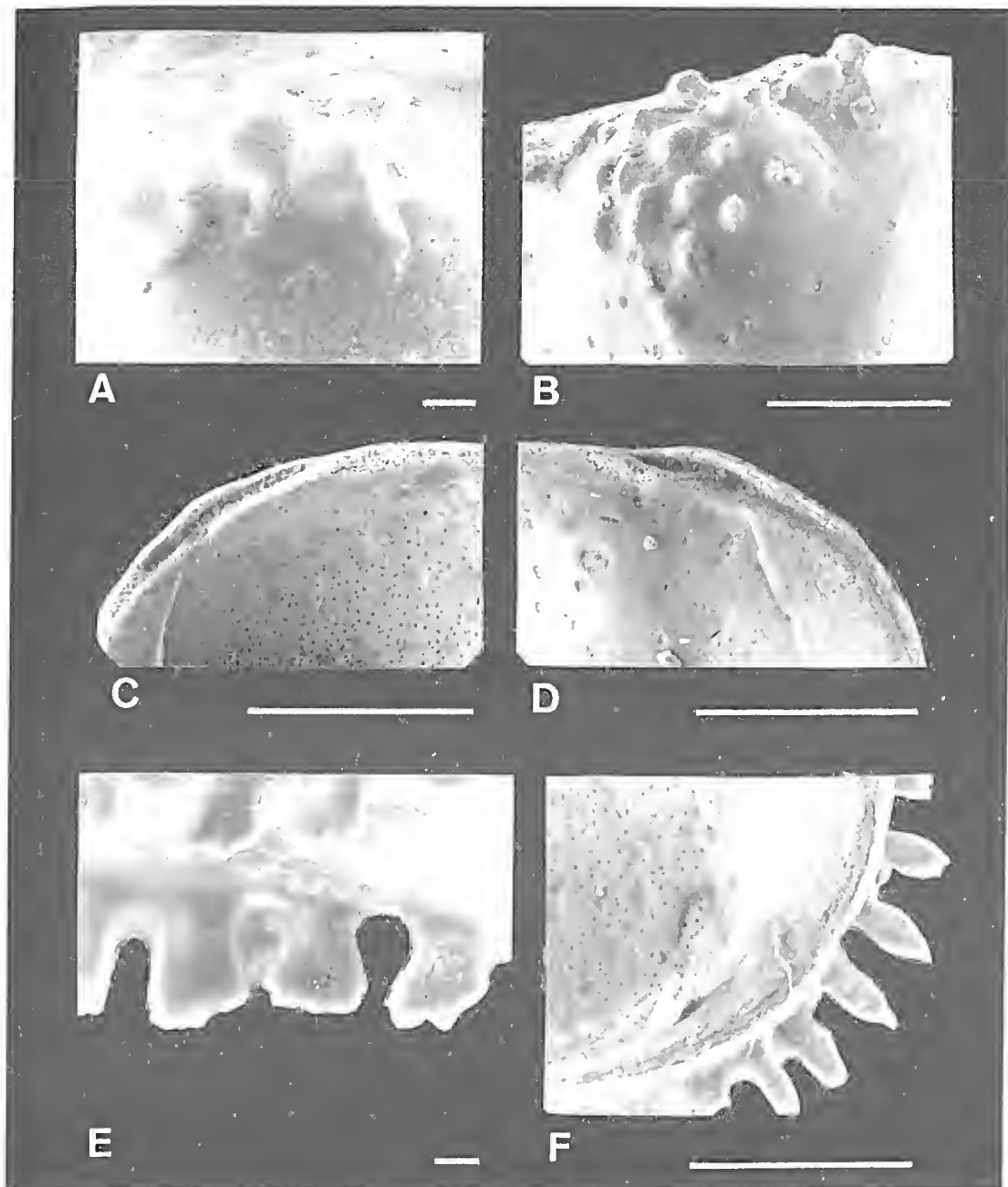
Fig. 3. A, C–F, *Miracythere* sp. A. A, spines on tubercle. C, posterior hinge line. D, anterior hinge line. E, spatulate spines on ventral margin. F, pointed spines on anteroventral margin. B, *Miracythere novaspecta* Hornibrook, 1952, pustules on tubercle. Scale bars = 0.01 mm in A and E, 0.1 mm in remainder.

Palaeozoic Kirkbyacea." Morphological simi-
larities between *Miracythere* and Palaeozoic
forms are less suggestive of phylogenetic links,
since the homologies are shared with a number
of Recent genera. Since *Miracythere* occurs only
in Recent and Tertiary sediments, as was be-
lieved to be the case for the punciids (Swanson,
1979b, 1985), the absence of Mesozoic records
of it or of *Kelletina* at present nullifies any hypo-
thetical phylogeny of *Miracythere* linking it with
the latter genus. The discovery of *Miracythere* in
Late Eocene sediments in a form possibly con-
specific with *Miracythere* sp. A gives an age
range in southeastern Australia greater than that
for *M. novaspecta* in New Zealand. This suggests
that the Mesozoic *Miracythere* gap might also be
filled in the course of further intensive collect-
ing, so that the possibility of an evolutionary
origin in a Palaeozoic kirkbyacean is not ruled
out. A more plausible view, however, is that the
basic morphology of *Miracythere* is the result of
convergent evolution of bythocytherids. The oc-
currence of ?*Miracythere* sp. in the Pleistocene
of New Zealand in a form which reflects some of
the characteristics of *Miracythere* sp. A whilst
differing markedly from *M. novaspecta* suggests
that a plexus of species of this genus may eventu-
ally be discovered.

ACKNOWLEDGEMENTS

REFERENCES

BERGGREN, W. A., KENT, D. Y. & VAN COUVERING, J.
    A., 1985. Neogene geochronology and chrono-
    stratigraphy. *Geological Society of London
    Memoir* 10: 211–260.
HARTMANN, G. & PURI, H. S., 1974. Summary of
    neontological and palaeontological classification
    of Ostracoda. *Mitteilungen aus dem Hambur-
    gischen Zoologischen Museum und Institut* 70:
    7–73.

HERRIG, E., 1988. Neue Ostrakoden aus Geschieben.
    *Geschiebekunde Actuell, Mitteilungen der
    Gesellschaft für Geschiebekunde* 4: 33–37.
HORNIBROOK, N. DE B., 1949. A new family of living
    Ostracoda with striking resemblances to some
    Palaeozoic Beyrichiidae. *Transactions of the
    Royal Society of New Zealand* 77: 469–471.
HORNIBROOK, N. DE B., 1952. Tertiary and Recent
    marine Ostracoda of New Zealand. *New Zeal-
    and Geological Survey, Palaeontological Bull-
    etin* 18: 1–82.
HORNIBROOK, N. DE B., 1963. The New Zealand ostra-
    code family Punciidae. *Micropaleontology* 9:
    318–320.
HORNIBROOK, N. DE B., 1968. A handbook of New
    Zealand microfossils (Formanifera & Ostra-
    coda). *Department of Scientific and Industrial
    Research, Information Series* 62: 1–136.
JENKINS, R. J. F., JONES, J. B., MCGOWAN, B.,
    BEECROFT, A. S. & FITZGERALD, M. J., 1982.
    Lithostratigraphic subdivision of the Blanche
    Point Formation, Late Eocene, Willunga Sub-
    basin. *Quarterly Geological Notes, Geological
    Survey of South Australia* 84: 2–7.
MCKENZIE, K. G. & NEIL, J. V., 1983. *Promanawa* gen.
    nov., an Australian Miocene punciid ostracode
    from Hamilton, Victoria. *Proceedings of the
    Royal Society of Victoria* 95: 59–64.
RUGGIERI, G. & SIVETER, D. J., 1975. On *Kelletina
    carnica* Ruggieri & Siveter sp. nov. *Stereo-Atlas
    of Ostracod Shells* 2: 215–222.
SCHORNIKOV, E. I., 1981. *Far-Eastern Marine Ostra-
    cods of the Family Bythocytheridae.* Nauka,
    Moscow, 199 p. (In Russian.)
SWAIN, F. M., 1967. Ostracoda from the Gulf of Cali-
    fornia. *Geological Society of America Memoir*
    101: 49.
SWAIN, F. M., 1983. Cretaceous Ostracoda from
    DSDP and IPOD deep-sea drilling sites. In *Ap-
    plications of Ostracoda. Proceedings of the
    Eighth International Symposium on Ostracoda,
    1982*, R. F. Maddocks, ed., Department of
    Geosciences, University of Houston, Texas,
    520–528.
SWANSON, K. M., 1979a. The marine fauna of New
    Zealand: ostracods of the Otago Shelf. *Memoirs
    of the New Zealand Oceanographic Institute* 78:
    1–56.
SWANSON, K. M., 1979b. In search of a living fossil.
    Scope 14 (5): 9–11.
SWANSON, K. M., 1985. The discovery of living pun-
    ciid ostracodes in New Zealand. *New Zealand
    Geological Survey Record* 9: 87–89.
SWANSON, K. M., 1991. Distribution, affinities and
    origin of the Punciidae (Crustacea: Ostracoda).
    Memoirs of the Queensland Museum 31: 77–
    92.

ECOLOGY OF TWO ASCLEPIAD LIANES IN SEMI-ARID VICTORIA

Kathy M. Nichols[1], J. H. Browne[2] and R. F. Parsons[1]

[1]Botany Department, La Trobe University, Bundoora, Victoria 3083
[2]52A Fitzroy Avenue, Red Cliffs, Victoria 3496

Nichols, K. M., Browne, J. H. & Parsons, R. F., 1991:12:31. Ecology of two asclepiad lianes in Victoria. *Proceedings of the Royal Society of Victoria* 103 (2): 93–112. ISSN 0035-9211.

Marsdenia australis and *Rhyncharrhena linearis* (Asclepiadaceae) are lianes of the "thin wiry" type. In Victoria they are found in semi-arid woodlands, secondary shrublands and mallee communities. Both can sucker profusely from the roots to form large clones but only *Marsdenia* has tuberous roots. Both species have a pair of foliar glands per leaf adaxially at the leaf base.

Fresh seed of both species has high germinability and most germinated in a few days, especially at 25°C. Germinability of *Marsdenia* seed declines with time and is zero at 14 yr. At 18 weeks old, *Marsdenia* seedlings have higher dry weights than those of *Rhyncharrhena* due to their well-developed tuberous root systems.

Although both species flower annually, there is regular November–December *Marsdenia* flowering, even in very dry conditions, whereas only a few *Rhyncharrhena* flowered after heavy rain within the January–April period during our study. Fruit set was low for both species, especially *Rhyncharrhena*. Both species showed some increase in shoot length from February to September; this is most rapid when rain falls during warm weather. During drought, *Rhyncharrhena* plants rapidly lost leaves while *Marsdenia* plants did not. Tuberous roots may allow *Marsdenia* to flower, fruit and retain leaves in conditions too dry for such behaviour in *Rhyncharrhena*. Both species are now vulnerable in Victoria. It is thought that the main threat is grazing by stock and rabbits. Fruiting has only been seen in plants which are climbing above 0.5 m in shrubs or trees; deliberate introduction of long-lived woody plants is needed to ensure seed production of *Marsdenia* and *Rhyncharrhena* in some grazing exclosures.

THE ASCLEPIADACEAE is a predominantly pan-tropical family of about 2000 species, mostly of woody climbers, perennial herbs and shrubs. The 60-odd Australian species occur mainly in the east and north, especially in rainforest, but a few species are widespread in semi-arid to arid areas and reach temperate latitudes (Williams 1984). Of the 12 or so important dicotyledonous liane families, Asclepiadaceae and Convolvulaceae (see below) are two which especially spread beyond rainforests into seasonally dry areas, both in Australia and elsewhere (Forster 1988, Hegarty 1989, Vahrmeijer 1981).

Lianes show decreasing robustness with decreasing annual rainfall; those dealt with here belong to the most slender of Webb's (1978) liane categories, being normally present as the "thin wiry" type (stem diameters less than 10 mm). In semi-arid north-western Victoria, there are seven native species which could be considered under this heading: *Marsdenia australis* and *Rhyncharrhena linearis* (Asclepiadaceae), *Jasminum didymum* ssp. *lineare* (Oleaceae), *Clematis microphylla* (Ranunculaceae) and *Convolvulus crispifolius, C. erubescens* and *C. remotus* (Convolvulaceae). Species nomenclature follows Ross (1990) except that the name *Marsdenia australis* (R. Br.) Druce has been preferred to *Leichardtia australis* R. Br. following recent revisionary studies suggesting that *Leichardtia* is a synonym of *Marsdenia* (P. I. Forster personal communication). Inclusion of the *Convolvulus* spp. on the above list may be contentious as similar *Convolvulus* species are treated by some authors as herbaceous, not woody, climbers (Pate & Dixon 1982, Keeley & Keeley 1988).

Of Australian asclepiads, only a small number of species from *Cynanchum, Marsdenia, Rhyncharrhena* and *Sarcostemma* occur in semi-arid to arid regions. They show various features thought to be xeromorphic, like leaflessness and succulence (*Sarcostemma*) or reduced leaves (e.g. *Rhyncharrhena*) (Lapinpuro 1976). The only such species occurring in Victoria, to be dealt with in detail below, are *Marsdenia australis* and *Rhyncharrhena linearis*. Other than these, the only native asclepiads in Victoria are

Fig. 1. Fruiting *Marsdenia australis* growing on *Dodonaea viscosa* at site 3 in March 1991.

Fig. 2. Fruiting *Rhyncharrhena linearis* growing on *Dodonaea viscosa* at site 1 in March 1991.

two species of *Marsdenia* and one of *Tylophora* in the rainforests and adjacent tall open-forests of East Gippsland 600 km to the south-cast.

The aim of this paper is to provide an introduction to the ecology of two asclepiads of arid and semi-arid areas, *Marsdenia australis* (Fig. 1) and *Rhyncharrhena linearis* (Fig. 2), at the temperate, southern limit of their range in Australia. *Rhyncharrhena* is one of only four asclepiad genera endemic to Australia, while *Marsdenia* is one of the most widespread genera, extending through parts of Asia, Africa and America. It is assumed that both *M. australis* and *R. linearis* were derived from northern Australian rainforest taxa in response to increasing aridity (Beadle 1981).

The work, nearly all in Victoria, is based on sporadic field observations from 1981 to 1989 and intensive work from January to December 1990. For brevity, the species will be referred to simply by their generic names. Two reasons for the project are (1) that both species have a con-

servation status rated as vulnerable Victoria-wide (Gullan, Cheal & Walsh 1990) so that data are needed as a basis for their management, and (2) that both were important aboriginal foods (Latz 1982) and *Marsdenia* in particular may be worth cultivating for its palatable fruits and its use as an indoor plant (Cherikoff & Isaacs no date, V. Cherikoff personal communication).

DISTRIBUTION AND HABITAT

Both species occur in inland parts of all mainland states of Australia including Queensland (Cunningham et al. 1981, Queensland Herbarium unpublished). There are records of both from at least as far north as 20°S, about the latitude of Tennant Creek (P. Latz personal communication) to as far south as 35°S near Walpeup in northwestern Victoria (this study).

Mean annual rainfall for both species can range from below 150 mm in the Great Victoria Desert (Greenslade, Joseph & Barley 1986) to above 400 mm in central New South Wales (Wilson 1980, Royal Botanic Gardens Sydney 1989). Seasonal rainfall distribution shows a slight May to October peak in Victoria (Badawy 1982) but changes to a summer maximum which becomes progressively more marked northwards (Slatyer 1962).

The whole area experiences hot summers and mild winters; mean temperatures increase steadily northwards. While frosts are very rare to absent north of 21°30′, mean annual frost frequency ranges from 7 to 32 in the area from Alice Springs to northwestern Victoria without correlating closely with latitude (Slatyer 1962, Australian Bureau of Meteorology unpublished data). Mean length of frost season is more

strongly related to latitude, reaching a maximum of 109 days in the south of the area in northwestern Victoria (Australian Division of National Mapping 1986, Badawy 1982). Given the recent emphasis on absolute minimum temperature in defining distribution limits (Woodward 1987, Booth 1990), such values range from 4.5°C at Tennant Creek, –7.5°C at Alice Springs, –2.8°C at Broken Hill, –4.0°C at Mildura, –5.8°C at Ouyen and –2.0°C at Walpeup (Australian Bureau of Meteorology unpublished screen temperatures).

Within the area studied in detail, northwestern Victoria, mean annual rainfall increases from 250 mm in the north (Neds Corner) to 343 mm in the south (Walpeup). Temperatures decrease and frost season increases at the same time; the areas south of about 35°S lacking *Marsdenia* and *Rhyncharrhena* are both wetter and colder than those areas supporting them (Badawy 1982). As growth of both species occurs especially in summer, decreased summer rainfall could possibly limit their distribution. However, there is no such decrease going from the north to the south of their Victorian range; some factor related to declining temperatures seems more likely to set their southern limits.

There is no clear evidence that the two species differ in their climatic tolerances.

A survey in 1985–6 of 1,300 20 m × 20 m quadrats in predominantly native vegetation in northwestern Victoria produced four records of *Marsdenia* and eight of *Rhyncharrhena* (Cheal & Parkes 1989 and personal communication), so these are not common species.

The Victorian distribution maps show 23 *Marsdenia* minor grid records and 15 of *Rhyncharrhena* (Fig. 3), partly reflecting the view that *Rhyncharrhena* is much the rarer of the two, e.g. in Victoria (J. N. Macfarlane personal communication) and around Broken Hill (Morris 1975).

In central Australia, most *Rhyncharrhena* plants are found in *Acacia aneura* communities, while *Marsdenia* occurs in most habitats (P. K. Latz 1982 and personal communication). However, in New South Wales both species occur in a wide range of communities, including those dominated by *Acacia aneura, Casuarina pauper, Eucalyptus intertexta* and various mallee species of eucalypt ("mallee") (Cunningham et al. 1981). In Victoria, the two asclepiads have very similar habitat ranges, both occupying relatively fertile sandy loams to clay loams carrying (1)
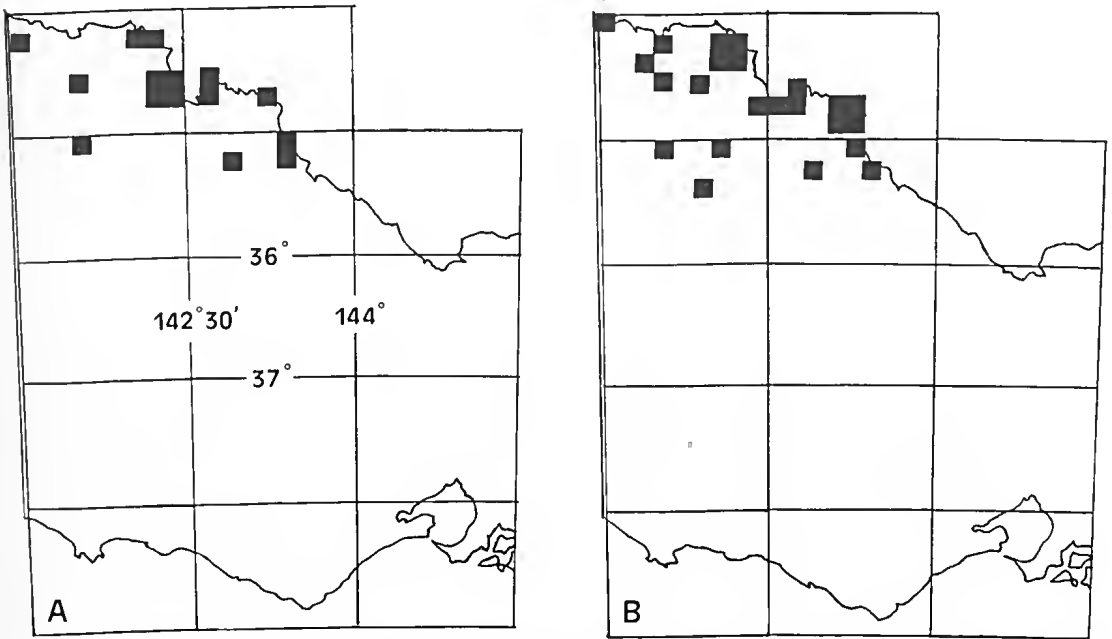

Fig. 3. Victorian distribution of (A) *Rhyncharrhena linearis* and (B) *Marsdenia australis* based on presence or absence within 10' latitude × 10' longitude grid squares for post-1950 records. All records from the Flora Survey and Management Group, Department of Conservation and Environment, with the addition of A31 and F29 for *M. australis*.

Site	Location[1]/management	Mean annual rainfall[2] (mm)	Area[4]	Topsoil texture	Plant community	No. of shoots seen in 1990 adults/suckers M	R
1	Department of Agriculture land, Campbell Avenue, Red Cliffs	285	8 ha	Sandy loam	*Cassia nemophila–Dodonaea viscosa* low shrubland[3]	22/20	39/70
2	Red Cliffs Scenic Reserve	285	21 ha	Sandy loam	*Cassia nemophila–Maireana pyramidata* low shrubland[3]	1/20	10/20
3	Red Cliffs Primary School Conservation Area	285	2 ha	Sandy loam	*Casuarina pauper–Callitris preissii* low woodland	9/15	3/10
4	Hattah–Kulkyne National Park	305	M 800 m² R 225 m²	Sandy loam	*Eucalyptus socialis* tall shrubland	1/10	1/100
5	Walpeup Flora & Fauna Reserve	343	50 m²	Sandy clay loam	*Eucalyptus dumosa* open scrub	13/20	None
6	Pink Lakes State Park	312	M 1156 m² R 1 ha	Sandy loam	M – Semi-cleared *Callitris preissii* low woodland R – Semi-cleared *E. socialis* tall shrubland	2/25	0/22

Table 1. Characteristics of Victorian *Marsdenia* and *Rhyncharrhena* sites examined in detail. [1] See Appendix 1 for details. [2] Using values from the Red Cliffs, Hattah, Walpeup and Underbool stations. [3] Secondary shrublands following clearance of woodlands like those at site 3. [4] M = *Marsdenia*, R = *Rhyncharrhena*.
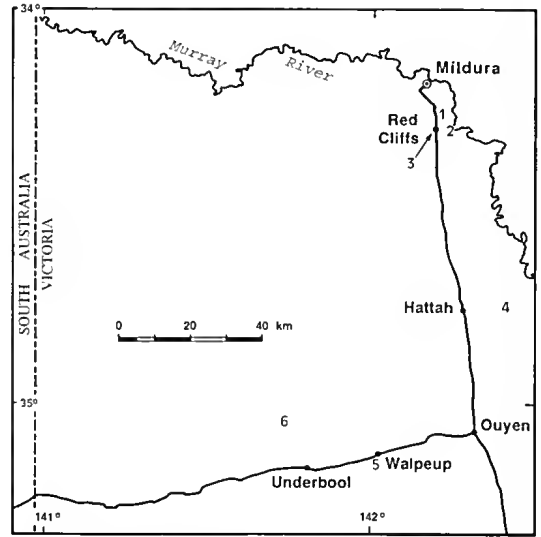

Fig. 4. Location of the study sites in north-western Victoria.

woodlands of *Casuarina pauper* and/or *Callitris preissii*, (2) various mallee communities or (3) various secondary shrublands following disturbance of (1) or (2) (see Table 1). They appear to be absent from the relatively infertile deep sands and from floodplains.

Sites for detailed study (Fig. 4) were chosen to encompass a range of mean annual rainfalls (Table 1, Appendix 1) and to include the largest populations known to us (sites 1, 3 and 5), as well as populations exclosed against grazing mammals in conservation reserves (sites 4 and 6).

MORPHOLOGY

Seed and seedling morphology

Marsdenia seeds are glabrous, dull, mid-to dark brown, flattened, finely winged, pyriform to ovate and comose at the narrower, germinating end. Germination is epigeal, the radicle emerging a minimum of two days from imbibition. Many short, fine root hairs develop as the radicle elongates (Fig. 5). The testa usually falls away in one piece. Sometimes it fails to fall off and dries, in which case it must be removed to allow seedling development as is the case in some other asclepiads (Harp 1987). The cotyledons are flat, petiolate and elliptical to obovate (Fig. 5). Tricotyledony occurs occasionally.

At 18 weeks, all seedlings have a tuberous taproot typically 10 mm in diameter with fine
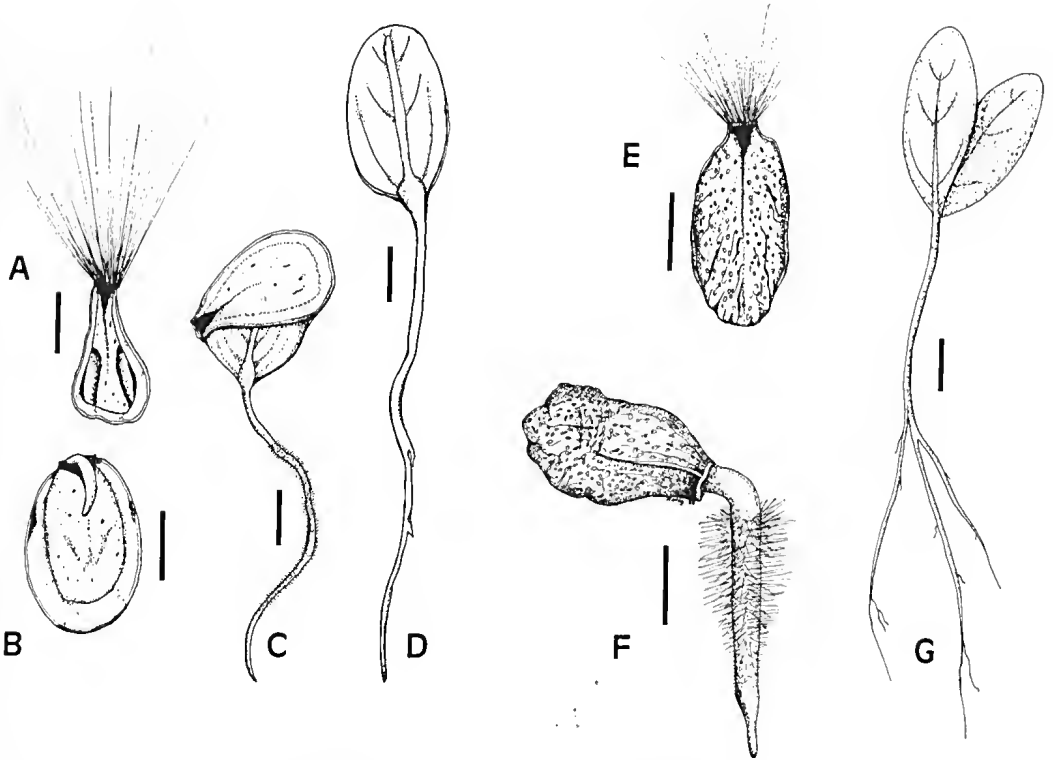
Fig. 5. Seeds and young seedlings of *Marsdenia australis* (A–D) and *Rhyncharrhena linearis* (E–G). A, E, dry seeds with comas. B, seed with radicle 2 days after sowing. C, F, seedlings 7 days after sowing showing root hairs. D, G, seedlings 12 days after sowing. Scale bars = 3 mm.

secondary roots (Fig. 6A) when the shoots are 440 mm tall.

On exceeding about 150 mm in height, the stem is unable to support the weight of the expanding leaves and bows over to become nearly horizontal; lateral shoots then develop from lower nodes. At this stage, the distal part of shoots can begin to revolve dextrorsely and to twine around any support encountered. Without support, the stem may bow almost to the ground and twine up about itself.

Rhyncharrhena seeds are rugulose, dull brown, flattened and elliptical to oblong. Germination and young seedling morphology are as for *Marsdenia* except for longer, denser root hairs and narrow-elliptical cotyledons (Fig. 5). No problem with persistent testas was found.

At 18 weeks, a root system lacking tubers is present (Fig. 6B); stem growth is similar to *Marsdenia*. There is no obvious ontogenetic change in leaf shape in either species.

Adult morphology

Shoots. Both species have opposite leaves lighter green and with denser stomata on the abaxial than on the adaxial surface. The stomata are modified rubiaceous type (Metcalfe & Chalk 1957).

Stem diameter was typically 5–7 mm and up to 10 mm in *Marsdenia*, but only 3 to 5 mm in *Rhyncharrhena*. When no support is found by circumnutating stems of either species, the stems can twine around themselves. In *Marsdenia* this can result in tightly plaited ropes up to 6 m long (Fig. 7); similar stems occur in the asclepiad *Aranjia sericofera* (Menninger 1970).

Like most Australian asclepiads, *Marsdenia* and *Rhyncharrhena* are apical stem twiners, a type of behaviour said to be seldom effective in climbing trees of over 100 mm diameter at breast height (Hegarty & Clifford 1984). In this study, we found them twining up a range of
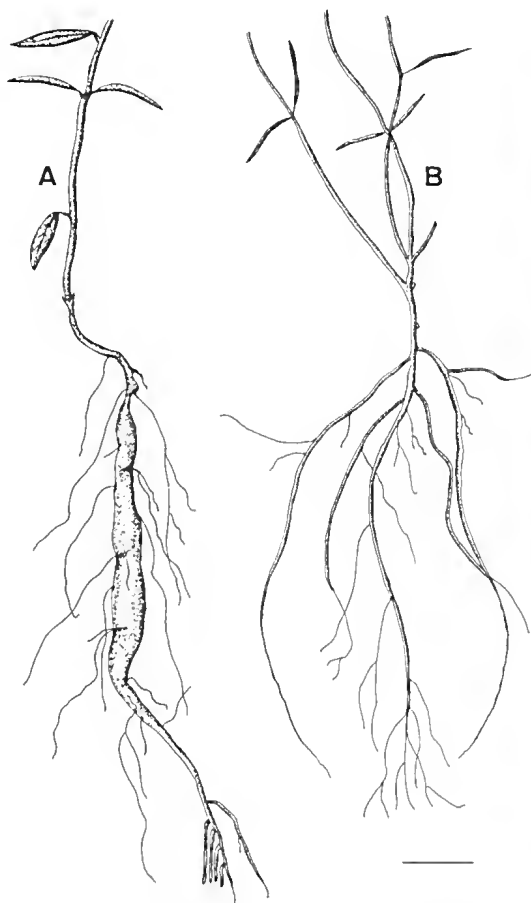
Fig. 7. *Marsdenia australis.* A plait of five stems 35 mm in diameter at site 5; the plant extends from the soil surface to the crown of a mallee species of *Eucalyptus* (stem visible in background).

Fig. 6. Eighteen-week-old seedlings of (A) *Marsdenia australis,* showing tuberous taproot and (B) *Rhyncharrhena linearis* with non-tuberous roots. Scale = 20 mm.

shrubs and mallee eucalypts, with *Marsdenia* twining up eucalypt trunks of up to 90 mm diameter and to heights of at least 4 m. Where *Marsdenia* and *Rhyncharrhena* occurred in *Callitris-Casuarina* woodlands, we found them on shrubs but not on the trees. While there are records from large trees (e.g. photograph of *Rhyncharrhena* on *Callitris,* Victorian reference set, National Herbarium of Victoria), it may be that such trees were climbed many years previously when they had thinner stems.

Internode lengths were shorter for unsupported lianes than supported ones and were generally shorter for *Marsdenia* than for *Rhyncharrhena*. It was common to find small, unsupported shoots scattered in the vicinity of large, supported plants in both species.

Roots and perennation. Parts of site 1 were excavated on 26–27 June 1990 to determine whether small, unsupported shoots were suckers or seedlings, and simultaneously to describe root systems.

Excavation of one adult *Marsdenia* plant and ten small shoots in an area of 2×1.5 m showed that all ten were suckers. Tissue sections showed that these arose from lateral roots. The suckers were from roots at depths of 100 mm to more than 500 mm below the surface and with diameters of 5 to 18 mm (Fig. 8A–C). They can occur more than 2 m from the parent plant.

Marsdenia has perennial tuberous roots, both laterals and tap-roots, the laterals up to 0.5 m long and 25 mm in diameter (Fig. 8A–C) and thus appreciably larger than those recorded in this species by Pate & Dixon (1982). The tuberous roots contain many large starch grains up to 10 μm in diameter; the stems have fewer, smaller grains (2.5 μm diameter). Copious branching leads to a complex system of tuberous
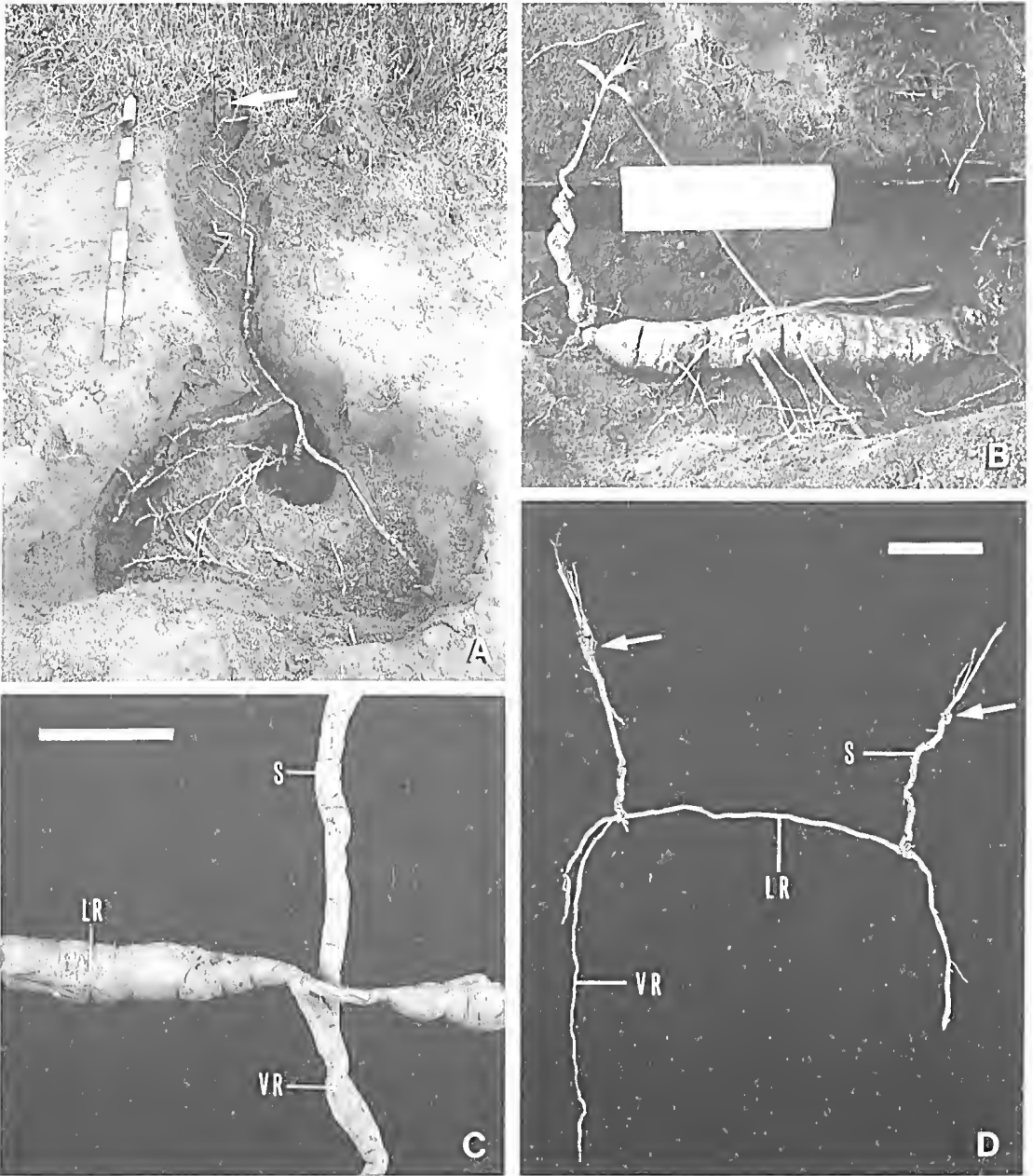
Fig. 8. A, partly-excavated root system of *Marsdenia australis* at site 1, showing tuberous horizontal and vertical roots. Arrow shows stem of adult plant. Scale divisions = 100 mm. B, part of *Marsdenia australis* plant at site 5, showing sucker shoot and tuberous root of 18 mm diameter. Scale divisions = 100 mm. C, part of *Marsdenia australis* plant at site 1 showing stem of sucker shoot (S), vertical root (VR) and tuberous root (LR) about 200 mm below soil surface. Scale = 30 mm. D, part of *Rhyncharrhena linearis* plant at site 1 showing two sucker shoots, stem (S), lateral root (LR), level of soil surface (arrow) and vertical root (VR). Scale = 50 mm.

roots in a number of layered, horizontal planes (Fig. 8A). Lateral tuberous roots were seen from 100 to 500 mm below the soil surface; vertical tuberous roots continued beyond 750 mm.

Tuberous roots are common in a number of liane families including the Asclepiadaceae, especially in species from seasonally dry areas rather than those from undisturbed evergreen rainforest (Hegarty 1989, Janzen 1975). Asclepiad examples include various African species of the succulent genus *Ceropegia* (Jacobsen 1960) and the Australian *Marsdenia flavescens, M. leptophylla* and *M. viridiflora* (Williams 1984).

Excavation of three small *Rhyncharrhena* shoots in an area of 500×200 mm showed them to be suckers, again from lateral roots (proved by tissue sections). Unlike *Marsdenia, Rhyncharrhena* roots are thin (diameter rarely greater than 5 mm) and non-tuberous, the laterals are not found deeper than about 200 mm and there is little branching (Fig. 8D). Starch grains are absent from the roots but present in the stems as before. Lines of sucker shoots strongly suggest that lateral roots can extend more than 15 m from parent plants (Fig. 9).

Root suckering, recorded here in *Marsdenia* and *Rhyncharrhena*, is known in other asclepiads, e.g. in *Morrenia odorata* (Tucker & Phillips 1974) and *Asclepias syriaca* (Bhowmik & Bandeen 1976) which can form clones of several thousand stems (Wilbur 1976). Such suckering may be "the most conspicuous form of asexual multiplication" in tropical perennials and may, for all we know, produce very large individual plants of great longevity, each spread over many hectares (Janzen 1975). Such suckering may allow some liane individuals, including *Marsdenia laxiflora*, to persist more or less indefinitely in the absence of regeneration from seed (Penalosa 1984). Other aspects of suckering are dealt with later.

Without data on root depth limits and location of soil moisture reserves, we are unable to classify *Marsdenia* and *Rhyncharrhena* root systems into types. Clearly both have extensive lateral roots. *Marsdenia* roots extend beyond 750 mm deep and Pate & Dixon (1982) treat the species as deep-rooted, but further data are needed.

ANATOMY

Methods

Seedling tissue 18 wk old was fixed in 5% glutaraldehyde in phosphate buffer, dehydrated in a graded ethanol series and then infiltrated with LR White resin ('BioRad' Microscience Division, Hemel Hempstead) over 72 hr and polymerized at 65°C overnight. Thick sections were obtained using an American Optical Corp. Model 860 sledge microtome and stained with 1% safranin (aqueous).

Fig. 9. Rhyncharrhena linearis sucker shoots marked with flags at site 4. Mature plant from which the suckers are probably derived is approximately 10 m to the left of the photo inside the fenced plot.

Stem

The stems of *Marsdenia* and *Rhyncharrhena* have a continuous vascular cylinder traversed by narrow rays (Fig. 10) as in many other asclepiads (Metcalfe & Chalk 1957). Both species have simple uniseriate hairs (Fig. 10A) and many druses attached to the wall of cortical cells (Fig. 10B). The cells of the hypodermis look very similar to those of the epidermis in both species.

Phloem occurs as small strands internal to the primary xylem (Fig. 10) in both species; such intraxylary phloem is universal in the family (Metcalfe & Chalk 1957). Some vessel elements have larger diameter in *Rhyncharrhena* than in *Marsdenia* (Fig. 10). Both species have thick-walled fibres adjacent to the external phloem. In both, broken cells indicate the natural disintegration of the central pith to produce a lysigenous cavity (Fig. 10).

While laticifers are thought to occur in the shoots of all asclepiads (Metcalfe & Chalk 1957), they can be difficult to distinguish (Metcalfe 1966) and we were unable to identify any with certainty. Cut stems exude milky latex in *Marsdenia* as in most asclepiads, but not in *Rhyncharrhena* which we assume has watery latex as seems to occur in *Asclepias tuberosa* (Wilbur 1976), *Ceropegia cumingiana* (Bruyns & Forster 1989) and some other asclepiads (Williams 1984).

Foliar glands

A number of plant species including asclepiads have foliar glands or squamellae adaxially at or near the leaf base (Ramayya & Bahadur 1968). As their nature in asclepiads is almost unknown, they were examined in *Marsdenia* and *Rhyncharrhena*.

Both *Marsdenia* and *Rhyncharrhena* have a pair of glands per leaf adaxially at the leaf base (Figs 11, 12). The glands are up to 0.3 mm long and exude copious amounts of a sticky, transparent substance through a large pore in the centre of the gland head (Fig. 11). Both stalk and head are nearly cylindrical but are more convex abaxially; the head sits obliquely on the stalk. Vascular tissue is absent. Necrotic cells on gland tips of older leaves may show that glands gradually cease to function once the leaves mature (see also Lapinpuro 1976).

In the closely-related Apocynaceae, the gland secretion is thought to be a high polymer resin and its suggested role is to provide a protective coating on adjacent young lateral buds (Ramayya & Bahadur 1968); this may apply also in *Marsdenia* and *Rhyncharrhena*. Such coatings might protect against climatic extremes in arid areas (Dell & McComb 1978) or against herbivores (Juniper & Jeffree 1983).

The anatomy and morphology of the glands are very similar to those of the other taxa examined in detail, both Apocynaceae (Ramayya & Bahadur 1968) and the asclepiad *Marsdenia liisae* (Lapinpuro 1976, Williams 1989).

GERMINATION

Methods

The coma was removed from seeds of known age and provenance (Appendix 2) and any broken, shrivelled or empty seeds discarded. Seeds were surface sterilized in 3% sodium hypochlorite and sown onto 9 cm Whatman 182 filter papers in sterile glass petri dishes, with five replicates of ten seeds per dish. The dishes were placed in growth cabinets with lights supplying $180–240\,\mu$ E m^{-2} s^{-1} for a 12 hr photoperiod at 10/10°C, 16/14°C, 25/15°C and (*Marsdenia* only) 30/20°C. For *Marsdenia* only, seed of four ages (Appendix 2) stored at room temperature and humidity was tested for germinability at 25/15°C. Comparable *Rhyncharrhena* seeds were not available.

Results and discussion

No seeds germinated at 10/10°C. For *Marsdenia*, final germination percentage was very similar at 25/15°C and 30/20°C but the germination rate was faster at 25/15°C. By comparison, 16/14°C reduced both the amount and the rate of germination in both species. Germination was highest and fastest in *Rhyncharrhena* at 25/15°C (Fig. 13).

Germinability of *Marsdenia* seed declined steeply with time and was zero at 14 yr (Fig. 14).

The germination maximum of 25/15°C for *Marsdenia* is broadly similar to that for other asclepiads like *Morrenia odorata* (20–25°C; Singh & Achhireddy 1984) and *Ampelamus albidus* (30°C; Soteres & Murray 1981). The present data for 10/10°C and 16/14°C suggest that germination may be reduced or prevented by winter temperatures in the field. All viable seeds of both species tend to germinate quickly given appropriate conditions; there is no evidence of dormancy as in some cool temperate species like *Asclepias syriaca* (Bhowmik & Bandeen 1976).
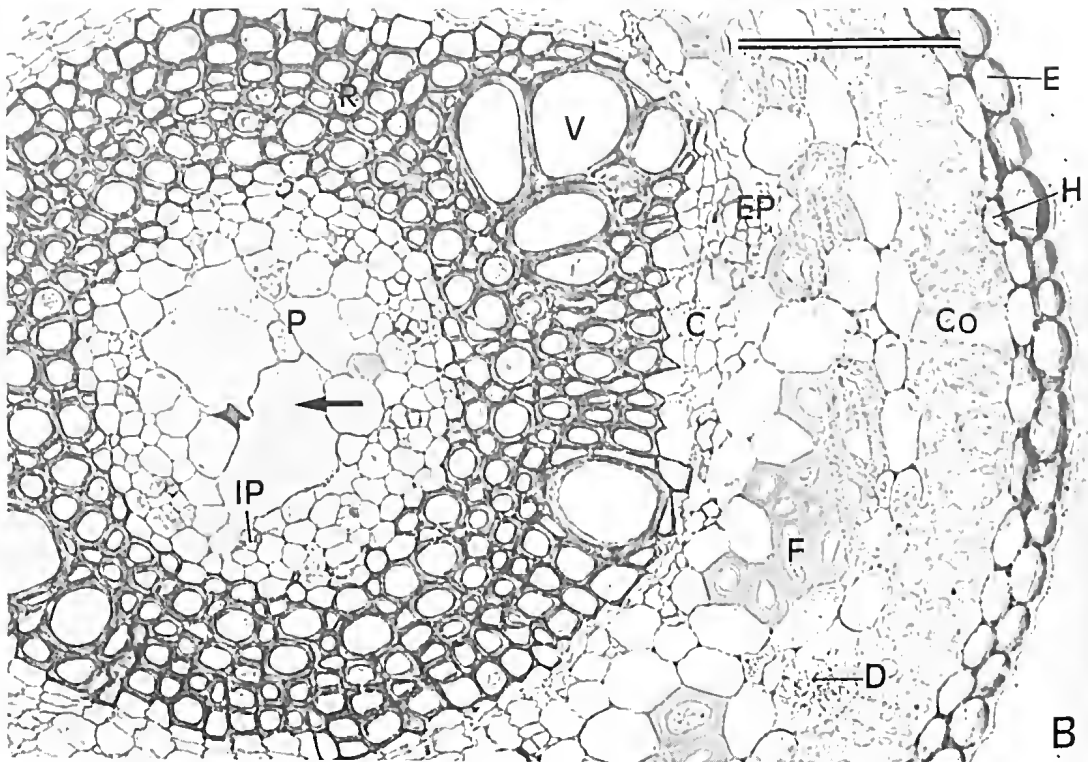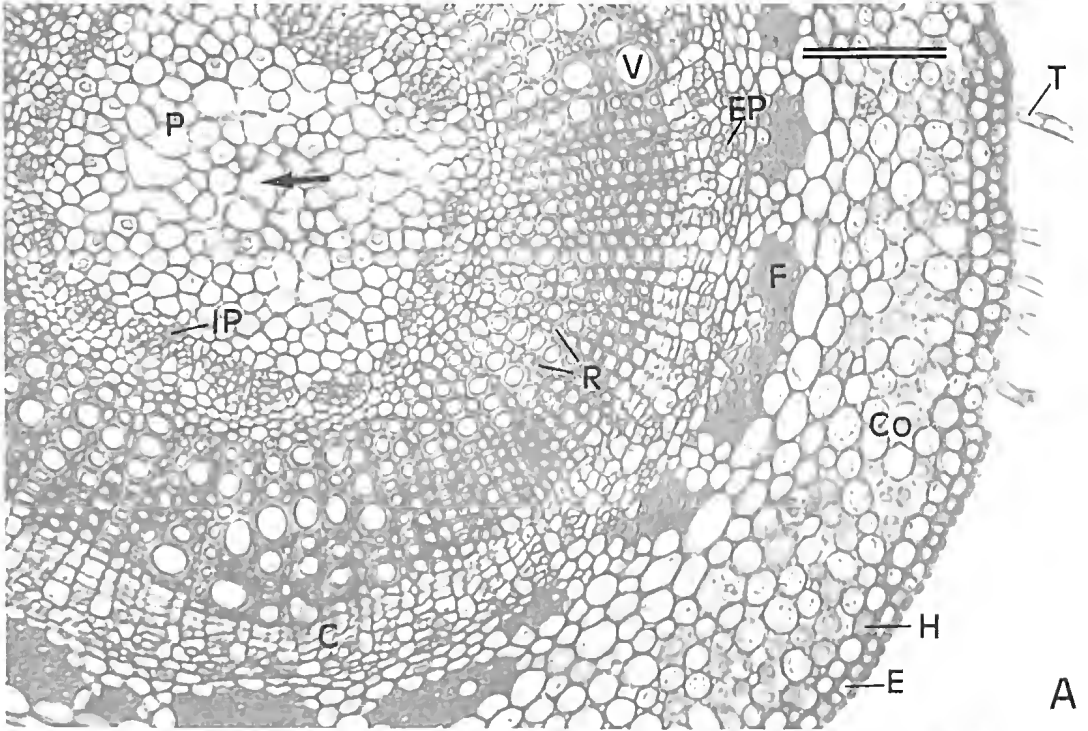
Fig. 10. Transverse sections of lower stems from approximately 18 week-old plants of *Marsdenia australis* (A) and *Rhyncharrhena linearis* (B), showing thick-walled epidermis (E) and hypodermis (H), trichome (T; cut short in sectioning), cortical chlorenchyma (Co), a druse (D), external phloem (EP) and phloem fibres (F), secondary xylem with vessels (V) and thickened rays (R), internal phloem (IP) and pith (P) with lysigenous cavities (arrowed). Scale bars = 0.1 mm.

The fast germination found here is similar to that found for a range of dry-country succulent asclepiads (Harp 1987).

SEEDLING GROWTH

Methods

Seedlings 5 to 15 days old were planted one per pot into 80×150 mm pots containing two parts sandy loam, one part vermiculite and one part perlite with controlled release fertilizer ('Nutricote', Chisso Asahi Co. Ltd, Tokyo, Japan) at the recommended rate. There were 10 replicates $\times$ 2 species $\times$ 2 treatments (16/14°C and 25/15°C). Otherwise growth cabinet conditions were as for the germination trials except for a 14 hr photoperiod. The seedlings were moved into the cabinets after four weeks at 25/15°C. None was given a support to climb on. All plants were dry-weighed at 105°C at an age of 18 wk.

Results and discussion

For all plants of both species introduced to 16/14°C, shoot growth rapidly slowed and then stopped. By contrast, 25/15°C produced rapid growth, with shoot length more than twice as long in *Rhyncharrhena* but shoot dry weight very similar in both species (Table 2). At 18 weeks, the *Marsdenia* seedlings at 25/15°C already had a well-developed tuberous root system while *Rhyncharrhena* had much thinner, non-tuberous roots. This difference correlated with much higher *Marsdenia* root dry weight which in turn resulted in higher total dry weight for that species (Table 2). While *Marsdenia* root weight increased 6.5 times from 16/14°C to 25/15°C, *Rhyncharrhena* increased less than twice. At 16/14°C the tubers of *Marsdenia* were very poorly developed. How this relates to climate and drought survival in the field requires further work.
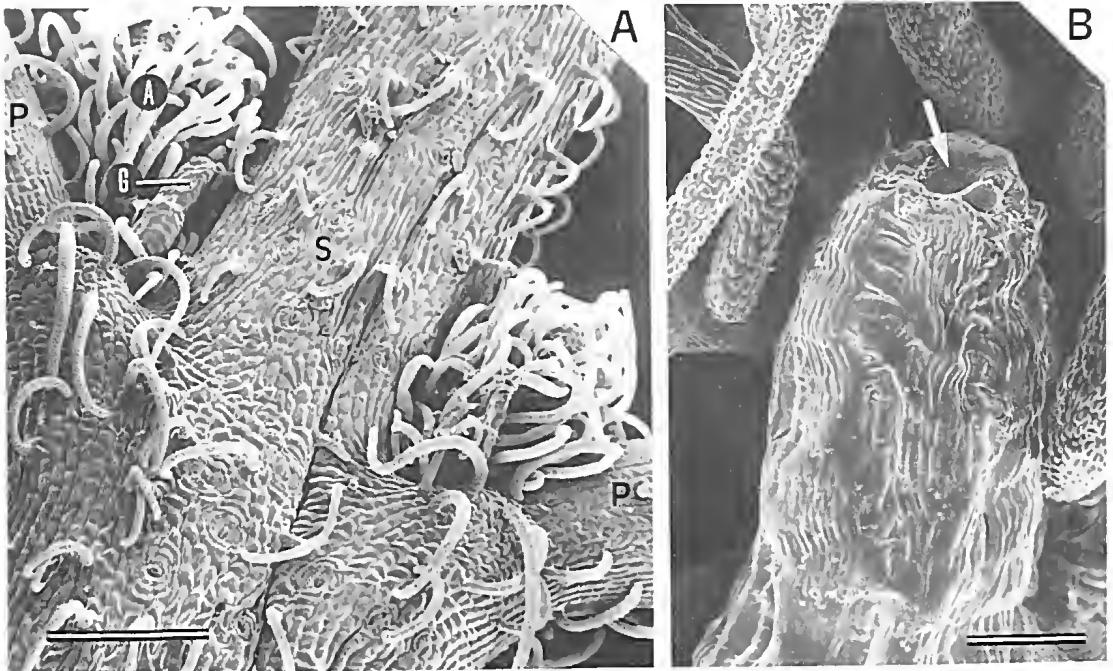

Fig. 11. A, scanning electron micrograph of a *Rhyncharrhena linearis* node, showing stem (S), petiole (P), axillary bud (A) and foliar gland (G). Scale = 0.03 mm. B, head of gland showing pore (arrowed). Scale = 0.3 mm.
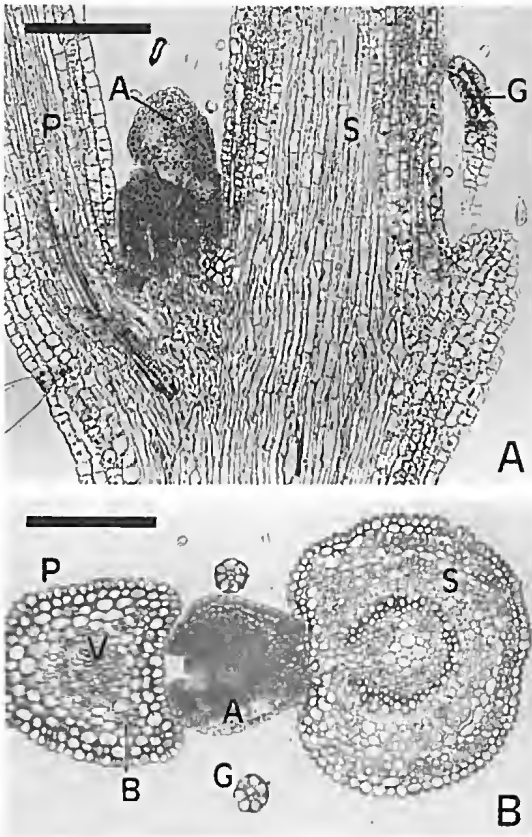
Fig. 12. A, longitudinal section through a stem node of *Rhyncharrhena linearis*, showing stem (S), petiole (P), an axillary bud (A) and a foliar gland (G) on the base of the opposite petiole. Scale = 0.2 mm. B, transverse section through a similar node, showing stem (S), axillary bud (A) and foliar gland stalk (G). The petiole (P), cut obliquely, has a crescent-shaped vascular strand (V) and accessory bundles (B). Note the radial arrangement of cells in the gland. Scale = 0.2 mm.

In summary, there are striking differences in seedling growth between the two species. The extra dry matter produced by *Marsdenia* is used for production of tuberous roots. Despite very similar shoot dry weights, *Marsdenia* produces thicker stems, larger leaves and a more rigid, erect shoot while *Rhyncharrhena* produces much longer, thinner shoots (Fig. 15). The reasons for these differences are obscure given the similarity between the two species in behaviour and habitat in the field.

The cessation of growth of both species at 16/14°C is like the behaviour of C_4 grasses at such temperatures (Evans et al. 1964). Given
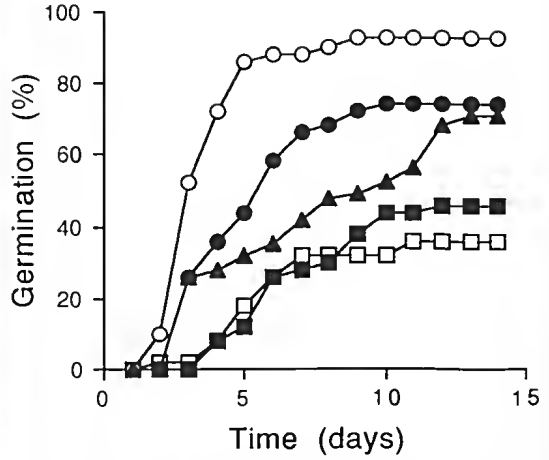
Fig. 13. Germination rate of *Marsdenia australis* and *Rhyncharrhena linearis* at various temperature regimes for seed 19 mo old. Open circles = *Rhyncharrhena* at 25/15°C, open squares = *Rhyncharrhena* at 16/14°C. Closed triangles, circles and squares = *Marsdenia* at 30/20°C, 25/15°C and 16/14°C respectively.
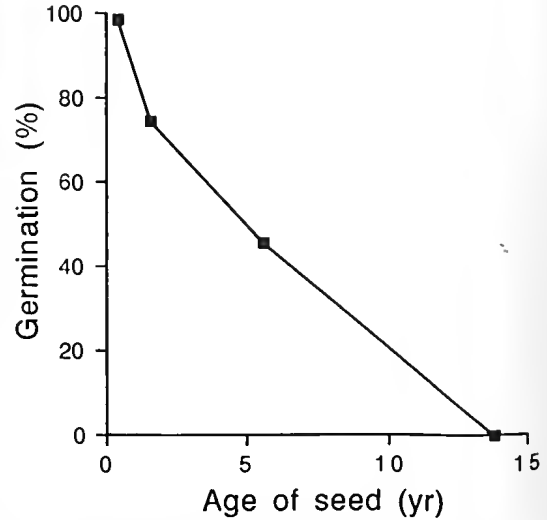
Fig. 14. Germinability of *Marsdenia australis* seeds of various ages at 25/15°C.

that the mean daily maximum temperature in June is about 16°C, the data suggest that little or no growth will occur in winter in the field. This is discussed further below.

These unsupported seedlings bowed over and grew more-or-less horizontally once they reached heights of 150 mm or so. We lack data

|	Marsdenia		Rhyncharrhena	
	16/14°C	25/15°C	16/14°C	25/15°C
Shoot length (mm)	66	436	199	1142
Dry weight (g)				
Shoot	0.14	1.57	0.15	1.58
Root	0.29	1.89	0.38	0.71
Total	0.43	3.46	0.53	2.29

Table 2. Mean shoot length and dry weight of 18 wk old *Marsdenia australis* and *Rhyncharrhena linearis* seedlings at two temperature regimes.

for supported young plants except for a single *Marsdenia* plant which twined 1.1 m up a stake in 10 weeks. Possible effects on growth caused by provision of support need investigating.

PHENOLOGY

Methods

General observations were made at all sites. At site 1, from 13 February to 23 May 1990, effects of water supply on shoot growth and flowering were studied by watering two *Marsdenia* and three *Rhyncharrhena* plants with a total of 600 L per plant via 22 L containers feeding a dripper system running at 400 mL/hr. Watering stopped

Fig. 15. Seven-week-old seedlings of *Marsdenia australis* (left) and *Rhyncharrhena linearis* (right) grown in a growth cabinet at 25/15°C.

in May when rainfall had clearly provided available water in the topsoil. Six unwatered control plants were monitored per species.

At site 2, from 19 February to 6 April 1990, one *Marsdenia* and three *Rhyncharrhena* were given 150 L of water each. One *Marsdenia* and three *Rhyncharrhena* were monitored as unwatered controls.

All plants monitored at sites 1 and 2 were more than 0.8 m high and were supported by shrub canopies. From 2 to 6 shoots per plant were tagged initially. Shoots were monitored until September 1990. Unfortunately it was logistically impossible to provide continuous watering to a larger number of plants. This factor, plus death of and damage to some shoots, produced very low replication in some cases, reducing the value of the experiment. Only a summary of the results is given below.

Results

Flowering and fruiting. Observations in the Red Cliffs district on similar numbers of plants of each species from 1981 to 1990 gave a flowering time range of October to March for *Marsdenia* and February to May for *Rhyncharrhena*. For the latter, however, buds can sometimes be seen even in July and September and we think it likely that flowering can occur from October to May (see also Cunningham et al. 1981, Jones & Gray 1988). In general, flowering for both occurs in the warmer months, especially when significant rain has fallen previously. However, *Marsdenia* is more likely to exhibit plentiful general flowering in December–January under a wide range of rainfall regimes. *Rhyncharrhena* seems to have a less definite flowering period; it seems more opportunistic, reacting more quickly with vigorous growth and flowering after significant summer–autumn rains. This species difference is dealt with more fully below. The smallest plants of both species seen flowering were about 600 mm high.
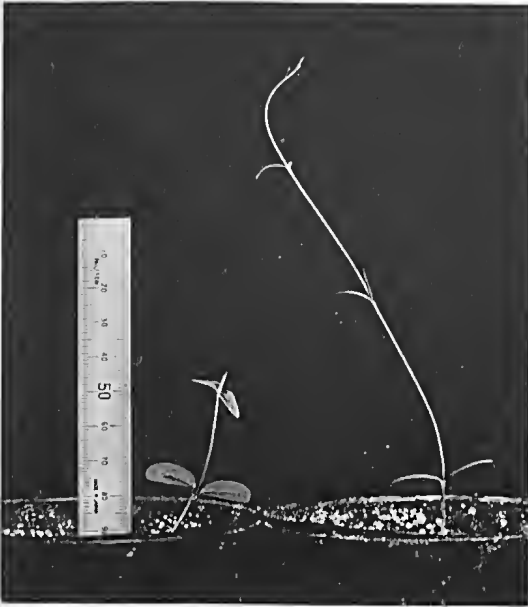
It is much more common for flowers of both species to wither and fall than to produce fruit; this can happen to *Rhyncharrhena* when *Marsdenia* is still flowering and fruiting at the same site. Although *Rhyncharrhena* flowered a number of times from 1981 to 1990, only five fruits (containing a total of 177 seeds) could be found, one in 1982 and four in 1989–90. Other than this, the only *Rhyncharrhena* fruiting records we know of are: (a) June 1950, after exceptional February–March rainfall of 177 mm (E. Ramsay, unpublished manuscript); and (b) March 1976, after exceptional October–December rainfall of 225 mm (our data). Finding as many as four fruits in 1989–90 was not due to heavy rain but because we started to examine repeatedly 48 adult plants; (a) and (b) above may indicate that appreciable levels of fruiting only follow exceptional rains.

Marsdenia fruiting is more common; for example 18 fruits could be found in 1984 and in 1990 38 adult plants under observation produced 15 fruits.

Number of seeds per fruit ranged from 37 to 213 for *Marsdenia* and 18 to 78 for *Rhyncharrhena*. Individual *Marsdenia* flowers remain open for seven to ten days and those of *Rhyncharrhena* for two to three days. This compares with five to six days for *Asclepias meadii* (Betz 1989), seven to eight days for *A. tuberosa* (Wyatt 1981) and 10–15 days for *Fischeria funebris* (Skutch 1988).

General phenology, 1989–1990. Following rain falls of 125 mm from 14 March to 7 April 1989, *Rhyncharrhena*, but not *Marsdenia*, flowered in mid-April. Virtually all these flowers were shed in late April without setting fruit.

No further flowering of either species occurred until above-average rain of 54 mm from 6 November to 2 December. By 14 December, shoot growth and flowering occurred profusely in all full-grown *Marsdenia* plants but not in any *Rhyncharrhena* plants.

In this area, 10 mm is the minimum rainfall that most farmers regard as being significant for plant growth in summer. There were no falls this large between 3 December 1989 and 21 April 1990. On 2 January 1990, with temperature maxima about 40°C, all *Rhyncharrhena* plants were either wilted or had started losing leaves. This was not true of *Marsdenia* except for some wilted sucker shoots. However, on 3 January 1990 temperatures reached 47°C, the hottest for 50 years; nearly all *Marsdenia* wilted and shed

their flowers except for those at site 3. The plants at site 3 shed most of their flowers a few days later. By 11 January, most *Marsdenia* shoots had recovered without damage. Between then and 25 January new shoot growth was noted for *Marsdenia* but not for *Rhyncharrhena* which showed further leaf loss and stem death and did not recover until April.

It was possible to obtain a few mature fruits of both species in January 1990; those of *Rhyncharrhena* probably arose from the April 1989 flowering while the origin of the *Marsdenia* fruits is unknown.

Detailed studies. At site 1, small flower buds were present on some plants of both species, especially *Rhyncharrhena*, before watering started. A second crop of *Rhyncharrhena* buds was present on 15 May following substantial rains. Despite these buds, throughout the work only a single plant of either species was seen with open flowers, a *Rhyncharrhena* in early March, and no fruit was set. Plants of both species, both watered and unwatered, showed some increase in shoot length and leaf number from February to September. This was most marked during April and May. The overall increases in mean shoot length to 4 August 1990 were: *Rhyncharrhena* (watered) 473 mm, *Rhyncharrhena* (unwatered) 133 mm, *Marsdenia* (watered) 197 mm and *Marsdenia* (unwatered) 229 mm. Although there was no statistically significant effect of watering, more data may have confirmed that *Rhyncharrhena* responds more strongly to watering than *Marsdenia*.

Events at the other sites from February to September 1990 were generally similar to those at site 1. The very few *Rhyncharrhena* that flowered included two plants at site 2 on 22 March, possibly in response to the artificial watering. The only *Marsdenia* to flower were three plants at site 5 on 6 March following 17 mm of rain. Despite the widespread *Marsdenia* flowering of December 1989, only at site 3 did fruit set occur, with a total of 10 fruits. A fruit cut open in June contained only immature seeds, while seeds from one cut open in August gave 100% germination. The remaining fruits finally opened naturally in mid-November 1990. This period of 11 months from flowering to seed release compares with two to four months from flowering to fruiting for *Sarcostemma esculentum* and *Gymnema geminatum* (Forster 1989) and about 3.5 months from pollination until fruits are ripe in *Asclepias meadii* (Betz 1989).

The period from pollination to seed release for three species of *Asclepias* ranges from about 2 to 4.5 months (Kephart 1987).

With increasing temperatures in September, most mature *Marsdenia* and *Rhyncharrhena* plants produced new crops of flower buds. The driest spring on record ensued (15 mm of rain at Mildura) and December was also very dry (4 mm). All *Rhyncharrhena* flower buds were lost but *Marsdenia* showed widespread flowering by mid-November. With very high January rainfall (87 mm), some flowers produced a crop of fruits 5 mm in diameter by 12 January and these became virtually full-sized by 2 February. A total of 49 full-sized fruits were counted at sites 1 and 3 on 13 February 1991.

By contrast, it was only after the 29 mm of rainfall on 5 January that *Rhyncharrhena* flowered (Fig. 16). It is assumed that this flowering produced the 20 well-developed fruits found at site 1 on 11 February. In central Australia, for both species, "significant fruiting only occurs after exceptional seasons or after fire" (P. K. Latz, personal communication).

The timing of events in *Marsdenia* is consistent over large areas; around Lindsay Point, 115 km to the west-north-west, *Marsdenia* also shed its seeds and flowered in November 1990 (R. Stoeckel, personal communication).

A major difference between *Marsdenia* and *Rhyncharrhena* is that in hot, dry periods during summer and autumn 1990 virtually all *Rhyncharrhena* plants lost at least some of their leaves, while no *Marsdenia* plants did. This was even more noticeable in the very dry late spring of 1990 when the few remaining *Rhyncharrhena* leaves were yellow and wilted while all *Marsdenia* leaves were still present and in good condition. The partial deciduousness of *Rhyncharrhena* may aid survival during drought (Russell-Smith & Dunlop 1987). While *Marsdenia* is regarded by Pate & Dixon (1982) as semi-deciduous if drought-stressed, we have never seen leaf loss at any time. Perhaps leaf loss occurs only in the most extreme conditions, possibly as a prelude to stem death (P. K. Latz, personal communication).
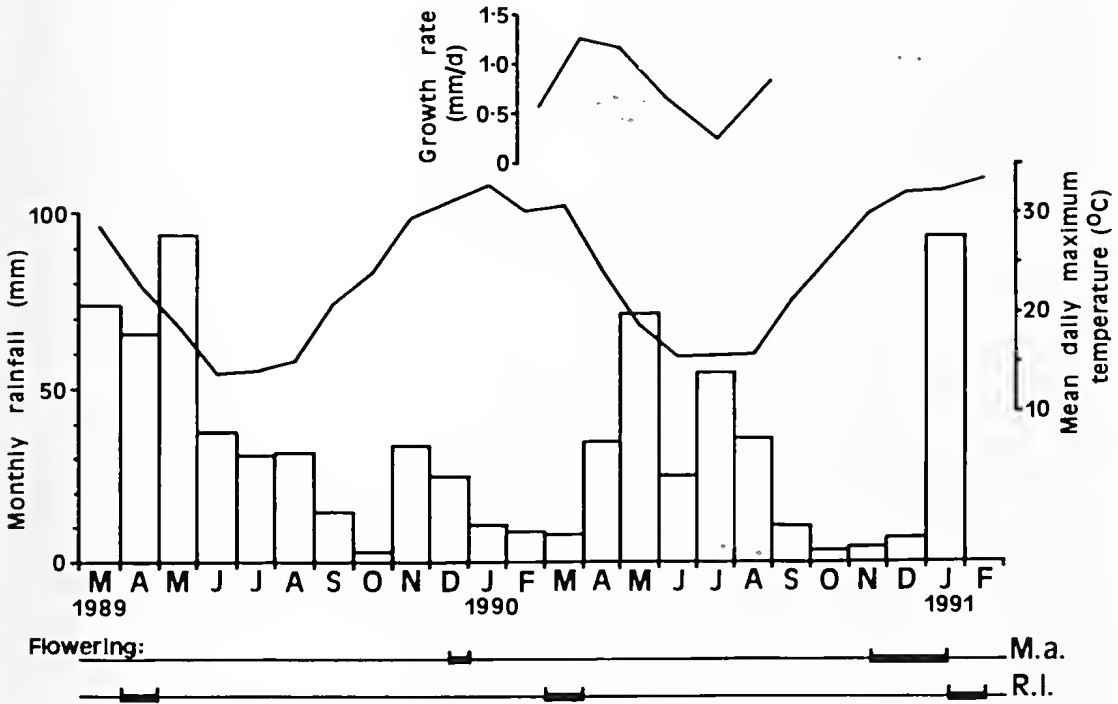
Although it is said that *Rhyncharrhena* can be

Fig. 16. Monthly rainfall (Red Cliffs), monthly means for daily maximum temperatures (Mildura), flowering times for *Marsdenia australis* and *Rhyncharrhena linearis,* and growth rate (shoot elongation) for unwatered *R. linearis* shoots at site 1 from February to September 1990.

short-lived in cultivation (Jones & Gray 1988), one of us (JHB) has observed individual plants of both species at Red Cliffs for more than 20 years. There has been no apparent size increase. It is possible that such plants may be very long-lived like those of other clonal species (Janzen 1975).

Discussion

Our observations suggest that some shoot growth occurred throughout the February–August period but that this was slow at the start and the finish, presumably due to low soil moisture and low temperatures respectively. Presumably shoot growth stops completely in very dry conditions like November–December 1990. Shoot growth is clearly much more vigorous in summer after thunderstorms or general rain than at other times.

In colder areas of southern Australia, introduced species of *Asclepias* are said to "die back when (night) temperatures drop below 0°C" and so to "disappear over winter" (Zalucki 1986). In our 1990 work, *Marsdenia* and *Rhyncharrhena* did not show any frost damage in a winter when the lowest absolute minimum screen temperature at Mildura was −1°C. Both are said to be tolerant of light to moderate frosts (Jones & Gray 1988). However, for *Marsdenia*, "foliage may dry off after frosts" (Griffin 1985), and in the winter of 1985 plants of both species growing on a fence at Sunny Cliffs showed frost damage while *Marsdenia* plants growing inside shrubs nearby were unaffected (personal observations).

The two species were strikingly different in flowering behaviour. In *Marsdenia* flowering (and fruiting) occurs on a much higher proportion of plants than in *Rhyncharrhena*. There was regular November–December flowering of *Marsdenia*, even in very dry conditions, whereas *Rhyncharrhena* flowering only followed heavy rain. It is not known why heavy autumn rain can produce flowering of *Rhyncharrhena* but not *Marsdenia*, as in 1989. In Queensland rainforest "almost all liane species flower once a year, in early summer" (Hegarty 1988). If individual *Marsdenia* plants flower annually, summer flowering would mean that few or no plants would flower in the succeeding autumn. Neither species flowers or fruits in the cold conditions of winter; it seems that amount of fruiting is related to rainfall at other times, especially summer. For both species, rainfall can be sufficient to produce flowering but be insufficient for any subsequent fruiting to occur.

Marsdenia flowering phenology was categorized by Pate & Dixon (1982) as "flowers produced annually during growth season".

It was hoped that artificial watering would produce widespread flowering and even fruiting, at least of *Rhyncharrhena*, but it only contributed to very limited flowering of that species. Watering a few shoots might not produce marked changes if those shoots were part of a very large clone covering most or all of the site, as is quite possible.

For both species, large numbers of sucker shoots up to 300 mm high can appear in open areas adjacent to mature plants. This is especially true in wet years like 1974–5, but plenty were found also in 1990 (Table 1). Before site 4 was fenced, *Rhyncharrhena* sucker shoots were grazed right off for three successive years, probably by kangaroos (T. Dominelli, personal communication). However, in unstocked areas near Red Cliffs lacking kangaroos and rabbits, large numbers of *Rhyncharrhena* suckers can appear after rain and then totally disappear during dry conditions, as they did in December 1990. In *Marsdenia*, only the smallest suckers die off during drought.

Most such suckers are found in open areas, often on perennial grasses or on live or dead annuals, but also in completely bare areas. In *Marsdenia*, such suckers can remain small but be many years old. For both species, in the absence of a substantial aerial support the suckers remain as small single shoots or die back; they do not form large, mature plants of shrub or creeper growth form, unlike *Jasminum didymum* (Cunningham et al. 1981, Hegarty & Clifford 1984).

Casual observations of supported and unsupported seedlings (see seedling growth section above) suggest the potential for very rapid height growth responses to provision of support, as is the case for rainforest lianes (Putz 1984).

Some of the striking phenological differences between *Marsdenia* and *Rhyncharrhena* may be because storage material in the tuberous roots of *Marsdenia* allows it to flower, fruit and retain leaves in conditions too dry for such behaviour in *Rhyncharrhena*. Work is needed to compare the water potential and intrinsic cellular resistance to desiccation of both species.

FLORAL BIOLOGY

Despite repeated observations, pollinators could not be found visiting flowers of either species. *Rhyncharrhena* is one of a number of asclepiads which has dark purple flowers (Good

1956). This feature and the presence of vibratile hairs on the flowers suggests that pollination may be by flies (Whittington 1989). Both *Marsdenia* and *Rhyncharrhena* flowers are odourless, at least in daytime.

All species in the family Asclepiadaceae studied in detail are obligate or nearly obligate outbreeders and exhibit low rates of fruit set, typically one to five per cent (see e.g. Holm 1950, Woodson 1954, Skutch 1988). These low rates can be related to low pollination rates and to energy limitation causing abscission of pollinated flowers and pod abortion (see e.g. Cabin et al. 1991, Pleasants 1991). Low rates of fruit set certainly apply also to *Marsdenia* and *Rhyncharrhena*. For a threatened prairie species of *Asclepias* now restricted to a few tiny refugia surrounded by farmland, problems may arise from (a) low populations of insect pollinators, and (b) insufficient plants to attract pollinators and maximize cross-pollination. Problem (b) can be exacerbated by extensive clones of the species causing extensive self-pollination (Betz 1989). These same problems may apply to many isolated *Marsdenia* and *Rhyncharrhena* stands in largely cleared Victorian areas.

Work on *Asclepias quadrifolia* shows that plants under the threshold of 330–340 mm stem height are unable to mature a fruit, any fruits initiated being aborted. Many small flowering plants apparently lack the energy resources to mature a fruit; only 20% of the flowering plants produce a fruit, production of which clearly depletes the plant's energy reserves (Chaplin & Walker 1982). *Marsdenia* and *Rhyncharrhena* seem to exhibit similar behaviour.

RESPROUTING

Fifty days after germination, ten plants each of *Marsdenia* and *Rhyncharrhena* were cut off below the cotyledons. Eight *Marsdenia* plants and all the *Rhyncharrhena* plants had resprouted 14 days later. Similarly, resprouting can occur in cut off 21-day-old *Asclepias syriaca* seedlings (Bhowmik & Bandeen 1976).

Patches of *Marsdenia* are known to persist in some areas of Victoria cleared of native vegetation in the 1920s; the small sucker shoots are repeatedly destroyed by ploughing or stock grazing but new ones continue to be produced by resprouting (J. N. Macfarlane, personal communication). Similar behaviour occurs in asclepiad weeds like *Asclepias syriaca* (Bhowmik & Bandeen 1976) and *Morrenia odorata* (Tucker & Phillips 1974). Such resprouting behaviour also

means that *Marsdenia* and *Rhyncharrhena* can occasionally be found climbing among the trees in commercial citrus groves, where irrigation can cause them to fruit prolifically (J. N. Macfarlane personal communication). Analogously, the asclepiad *Morrenia odorata* is a major weed of Florida citrus groves (Tucker & Phillips 1974).

Post-fire behaviour of *Marsdenia* and *Rhyncharrhena* has not been seen in Victoria. In central Australia, vigorous resprouting can make both species conspicuous after fire, they being among the first species to appear. Later in the post-fire period, increased competition from other perennial species can make them less conspicuous and reduce or prevent their fruiting (Latz 1982 and personal communication). Resprouting allows other asclepiads to tolerate frequent low-intensity fires in monsoon areas further north (Russell-Smith & Dunlop 1987).

RESPONSES TO GRAZING

The Asclepiadaceae is noted for presence of toxic cardiac glycosides, alkaloids and resinoids. As a result, many species are extremely unpalatable to grazing mammals and are generally avoided by them (Everist 1974). For example, severe overgrazing by goats can produce monospecific communities of the poisonous asclepiad *Calotropis procera* (Kassas 1966). Despite this, it is thought that mammal grazing can dramatically reduce *Marsdenia* and *Rhyncharrhena* populations. In Victoria, by 1937 *Marsdenia* was "rapidly becoming rarer" because it was especially palatable to rabbits, which ate the foliage and removed the bark from stems near the ground (Zimmer 1946).

Both species are now very rare virtually throughout their former range in Victoria (see Table 1). For example, only two adult plants of *Marsdenia* are now known in Hattah–Kulkyne National Park and there are only three recent records from the whole of the Sunset Country. The only populations of any size are from unstocked areas close to towns (sites 1 and 3, Red Cliffs; site 5, Walpeup) where rabbit (and other grazing mammal) numbers remain low, possibly due to factors like predation from domestic cats and dogs. *Rhyncharrhena* behaves similarly (Table 1). In some parts of the ranges of both species, grazing by hares may be more important than that by rabbits (J. N. Macfarlane personal communication).

In western New South Wales *Rhyncharrhena* is grazed readily by sheep. Under grazing "the

only plants which appear to survive are those which have the stem closely pressed to the bark of a tree or are growing up through a groove in the bark" (W. E. Mulham, personal communication). In central Australia *Marsdenia* is noticeably rarer in the area of highest rabbit numbers, namely the south west corner where rabbit grazing has apparently severely reduced the species (Latz 1982).

A similar case of a marked grazing effect on a liane concerns the eastern Victorian *Parsonsia brownii* in the closely related family Apocynaceae. *P. brownii* is especially palatable to wallabies and normally only scattered plants of it can be found. Where wallabies are absent, however, as in some very small remnants of native vegetation or in reserves surrounded by suburbs, dense stands of *P. brownii* develop (Ashton 1989; N. H. Scarlett, personal communication). The New Zealand *P. heterophylla* is especially palatable to a browsing bird (Clout & Hay 1989).

DISPERSAL

Both *Marsdenia* and *Rhyncharrhena* have typical asclepiad seeds with a terminal coma of long hairs. In *Asclepias syriaca*, these hairs allow wind dispersal at distances of up to 150 m and further (Morse & Schmitt 1985), and in *Araujia sericofera* such dispersal allows the species "to arrive in almost every Auckland garden" (Esler 1988). There is no evidence that *Marsdenia* or *Rhyncharrhena* seeds are predated by birds or ants.

CONSERVATION

While not threatened Australia-wide, both *Marsdenia* and *Rhyncharrhena* are now regarded as vulnerable in Victoria (Gullan et al. 1990). The apparent severe decline under grazing, the absence of seedling establishment, the lack of information on the lifespan of the remaining adult plants and the very small number of adults in biological reserves are all causes for concern. Although *Rhyncharrhena* is recorded from a total of four Victorian reserves (Beauglehole 1979), in each case only a few plants are present (A. C. Beauglehole and J. N. Macfarlane, personal communications). *Marsdenia* is a very similar case, being regarded even in 1937 as "likely to become extinct" (Zimmer 1946).

Conservation work so far has involved fencing small patches of both species at Hattah–Kulkyne

National Park (site 4) and Pink Lakes State Park (site 6), and at the latter providing small tree guards about 300 mm high for *Rhyncharrhena* suckers. We only saw fruiting of either species occur when the plants were climbing in shrubs or trees; although increased shoot growth occurred when the tree guards were installed, no fruit was set. Grazing exclosures for the species should include long-lived trees or shrubs if possible; if none are present, it may be necessary to introduce them to make the exclosure worthwhile in the long-term.

ETHNOBOTANY

In central Australia *Marsdenia* and *Rhyncharrhena* were important and favoured aboriginal foods, all parts being used except the stems and fine roots. The aborigines were aware that a diet containing a high proportion of *Rhyncharrhena* caused their children to lose weight (Latz 1982). The ground-up seeds of both species are reputed to have been used as an oral contraceptive (Lassak & McCarthy 1983).

The immature fruits of *Marsdenia* are so delicious that the species may be worthwhile cultivating (Cherikoff & Isaacs, no date; V. Cherikoff, personal communication).

REFERENCES

ASHTON, D. H., 1989. Restore Sherbrooke's ecological balance. Letter to the editor, *The Age*, Melbourne, 13 January 1989.

AUSTRALIAN DIVISION OF NATIONAL MAPPING, 1986. *Atlas of Australian Resources,* 3rd series, vol. 4, *Climate.* Division of National Mapping, Canberra.

BADAWAY, N. S., 1982. Soils of north-western Victoria, their characteristics and significance to local agriculture. Victorian Department of Agriculture, Technical Report Series No. 55.

BEADLE, N. C. W., 1981. *The Vegetation of Australia.* Cambridge University Press.

BEAUGLEHOLE, A. C., 1979. *The Distribution and Conservation of Native Vascular Plants in the*

Victorian Mallee. Western Victorian Field Naturalists Clubs Association, Portland.

BETZ, R. F., 1989. Ecology of Mead's milkweed (*Asclepias meadii* Torrey). In *Proceedings of the Eleventh North American Prairie Conference*, T. B. Bragg & J. Stubbendieck, eds., University of Nebraska, Lincoln, 187–191.

BHOWMIK, P. C. & BANDEEN, J. D., 1976. The biology of Canadian weeds. 19. *Asclepias syriaca* L. *Canadian Journal of Plant Science* 56: 579–589.

BOOTH, T. H., 1990. Mapping regions climatically suitable for particular tree species at the global scale. *Forest Ecology and Management* 36: 47–60.

BRUYNS, P. V. & FORSTER, P. I., 1989. *Ceropegia cumingiana* Decne (Asclepiadaceae). *Austrobaileya* 3: 7–11.

CABIN, R. J., RAMSTETTER, J. & ENGEL, R. E., 1991. Reproductive limitations of a locally rare *Asclepias. Rhodora* 93: 1–10.

CHAPLIN, S. J. & WALKER, J. L., 1982. Energetic constraints and adaptive significance of the floral display of a forest milkweed. *Ecology* 63: 1857–1870.

CHEAL, D. C. & PARKES, D. M., 1989. Mallee vegetation in Victoria. In *Mediterranean Landscapes in Australia*, J. C. Noble & R.A. Bradstock, eds. CSIRO, Melbourne, 125–140.

CHERIKOFF, V. & ISAACS, J., NO DATE. *The Bush Food Handbook*. Ti Tree Press, Sydney.

CLOUT, M. N. & HAY, J. R., 1989. The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. *New Zealand Journal of Ecology* 12 (Supplement): 27–33.

CUNNINGHAM, G. M., MULHAM, W. E., MILTHORPE, P. L. & LEIGH, J. H., 1981. *Plants of Western New South Wales*. New South Wales Government Printing Office, Sydney.

DELL, B. & McCOMB, A. J., 1978. Plant resins – their formation, secretion and possible functions. *Advances in Botanical Research* 6: 278–316.

ESLER, A. E., 1988. The naturalisation of plants in urban Auckland, New Zealand. 4. *New Zealand Journal of Botany* 26: 345–385.

EVANS, L. T. WARDLAW, I. F. & WILLIAMS, C. N., 1964. Environmental control of growth. In *Grasses & Grasslands*. C. Barnard, ed., Macmillan, London, 102–125.

EVERIST, S. L., 1974. *Poisonous Plants of Australia*. Angus & Robertson, Sydney.

FORSTER, P. I., 1988. The genus *Sarcostemma* R. Br. (Asclepiadaceae) in Australia. *Anacampseros* 4: 73–79.

FORSTER, P. I., 1989. Notes on Asclepiadaceae, I. *Austrobaileya* 3: 109–133.

GOOD, R., 1956. *Features of Evolution in the Flowering Plants*. Longmans, Green, London.

GREENSLADE, P., JOSEPH, L. & BARLEY, R., 1986. *The Great Victoria Desert*. Nature Conservation Society of South Australia, Adelaide.

GRIFFIN, G., 1985. Bushtucker. *Australian Plants* 13: 127–134.

GULLAN, P. K., CHEAL, D. C. & WALSH, N. G., 1990. *Rare or Threatened Plants in Victoria*. Victorian Department of Conservation & Environment, Melbourne.

HARP, C., 1987. Raising asclepiads from seed. *Asklepios* 41: 11–13.

HEGARTY, E. E., 1988. Canopy dynamics of lianes and trees in subtropical rainforest. PhD thesis, University of Queensland.

HEGARTY, E. E., 1989. The climbers – lianes and vines. In *Tropical Rain Forest Ecosystems. B. Biogeographical and Ecological Studies*, H. Leith & M. Werger, eds, Elsevier, Amsterdam, 339–353.

HEGARTY, E. E. & CLIFFORD, H. T., 1984. Climbing angiosperms in the Australian flora. In *Australian National Rainforest Study Report to the World Wildlife Fund*, G. Werren & A. P. Kershaw, eds, Geography Department, Monash University, Melbourne, 238–263.

HOLM, R. W., 1950. The American species of *Sarcostemma* R. Br. (Asclepiadaceae). *Annals of the Missouri Botanical Garden* 37: 477–560.

JACOBSEN, H., 1960. *A Handbook of Succulent Plants*, vol. 1. Blandford Press, London.

JANZEN, D. H., 1975. *Ecology of Plants in the Tropics*. Arnold, London.

JONES, D. L. & GRAY, B., 1988. *Climbing Plants in Australia*. Reed, Sydney.

JUNIPER, B. E. & JEFFREE, C. E., 1983. *Plant Surfaces*. Arnold, London.

KASSAS, M., 1966. Plant life in deserts. In *Arid Lands*. E. S. Hills, ed., Methuen, London, 145–179.

KEELEY, J. E. & KEELEY, S. C., 1988. Chaparral. In *North American Terrestrial Vegetation*. M. G. Barbour & W. D. Billings, eds, Cambridge University Press, 175–184.

KEPHART, S. R., 1987. Phenological variation in flowering and fruiting of *Asclepias. American Midland Naturalist* 118: 64–76.

LAPINPURO, M. L., 1976. Studies in the taxonomy, ecology and anatomy of the Asclepiadaceae of north-eastern New South Wales. BSc (Honours) thesis, University of New England.

LASSAK, E. V. & McCARTHY, T., 1983. *Australian Medicinal Plants*. Methuen, Sydney.

LATZ, P. K., 1982. Bushfires and bush tucker. MSc thesis, University of New England.

MENNINGER, E. A., 1970. *Flowering Vines of the World*. Hearthside Press, New York.

METCALFE, C. R., 1966. Distribution of latex in the plant kingdom. *Economic Botany* 21: 115–125.

METCALFE, C. R. & CHALK, L., 1957. *Anatomy of the Dicotyledons*, vol. 2. Oxford University Press.

MORRIS, A., 1975. *Plantlife of the West Darling*. 2nd edn. Barrier Field Naturalists Club, Broken Hill.

MORSE, D. H. & SCHMITT, J., 1985. Propagule size,

dispersal ability and seedling performance in *Asclepias syriaca. Oecologia* 67: 372–379.

PATE, J. S. & DIXON, K. W., 1982. *Tuberous, Cormous and Bulbous Plants.* University of Western Australia Press, Perth.

PENALOSA, J., 1984. Basal branching and vegetative spread in two tropical rain forest lianes. *Biotropica* 16: 1–9.

PLEASANTS, J. M., 1991. Evidence for short-distance dispersal of pollinia in *Asclepias syriaca* L. *Functional Ecology* 5: 75–82.

PUTZ, F. E., 1984. The natural history of lianes on Barro Colorado Island, Panama. *Ecology* 65: 1713–1724.

Ross, J. H., 1990. *A Census of the Vascular Plants of Victoria,* 3rd edn. National Herbarium of Victoria, Melbourne.

ROYAL BOTANIC GARDENS SYDNEY, 1989. *Annual Report 1988–1989.* Royal Botanic Gardens, Sydney.

RUSSELL-SMITH, J. & DUNLOP, C., 1987. The status of monsoon vine forests in the Northern Territory: a perspective. In *The Rainforest Legacy,* Australian Heritage Commission Special Australian Heritage Publication Series No. 7, Canberra, 227–253.

SINGH, M. & ACHHIREDDY, N. R., 1984. Germination ecology of milkweedvine (*Morrenia odorata*). *Weed Science* 32: 781–785.

SKUTCH, A. F., 1988. Flowering and seed-production of *Fischeria funebris* (Asclepiadaceae). *Brenesia* 30: 13–17.

SLATYER, R. O., 1962. Climate of the Alice Springs area. In *Lands of the Alice Springs Area, Northern Territory, 1956–1957,* CSIRO Australia Land Research Series No. 6, 109–128.

SOTERES, J. K. & MURRAY, D. S., 1981. Germination and development of honeyvine milkweed (*Ampelamus albidus*) seed. *Weed Science* 29: 625–628.

TUCKER, D. & PHILLIPS, R., 1974. The strangler vine: a major weed pest in Florida citrus groves. *Weeds Today,* December 1974: 6–8.

VAHRMEIJER, J., 1981. *Poisonous Plants of Southern Africa.* Tafelberg, Cape Town.

WEBB, L. J., 1978. A general classification of Australian rainforests. *Australian Plants* 9: 349–363.

WHITTINGTON, A. E., 1989. A short comparative biology of two stapeloid plants. *Veld and Flora* 75: 126–129.

WILBUR, H. M., 1976. Life history evolution in seven milkweeds of the genus *Asclepias. Journal of Ecology* 64: 223–240.

WILLIAMS, J. B., 1984. Family 143. Asclepiadaceae. In *Student's Flora of North Eastern New South Wales,* N. C. W. Beadle, ed., Botany Department, University of New England, Armidale, 703–734.

WILSON, K. L., 1980. The genus *Rhyncharrhena* (Asclepiadaceae). *Telopea* 2: 35–39.

WOODSON, R. E., 1954. The North American species of *Asclepias* L. *Annals of the Missouri Botanical Garden* 41: 1–211.

WOODWARD, F. I., 1987. *Climate and Plant Distribution.* Cambridge University Press.

WYATT, R., 1981. The reproductive biology of *Asclepias tuberosa.* II. *New Phytologist* 88: 375–385.

ZALUCKI, M. P., 1986. The monarch butterfly – a non-pest exotic insect. In *The Ecology of Exotic Animals and Plants,* R. L. Kitching, ed., Wiley, Brisbane, 129–136.

ZIMMER, W. J., 1946. *The Flora of the Far North-West of Victoria.* Forests Commission of Victoria Bulletin no. 2.

APPENDIX 1

Location of the study sites; see also Table 1.

Site 1. 34°20′S, 142°20′E. All plants studied were less than 50 m W of Campbell Avenue. *Rhyncharrhena* sites on ridge 0.3 km N of 22nd Street. *Marsdenia* sites on ridge 0.3 km farther N.

Site 2. 34°21′S, 142°21′E. W side of main N–S track through reserve, 0.1–0.3 km SE of the intersection of the track and Woomera Avenue.

Site 3. 34°48′S, 142°17′E. S side of Nardoo Street, Red Cliffs. The plants are scattered through the least disturbed area.

Site 4. 34°48′S, 142°17′E. (a) *Marsdenia.* Plot 0.6 km along Jasmine Track from its N end, then 0.2 km WSW of track. (b) *Rhyncharrhena.* National Parks Service plot no. 9E, 0.8 km along Jasmine Track from its N end, then 28 m W of track.

Site 5. 35°10′S, 142°2′E. In the western block of the reserve, 0.5 km S of Ouyen Highway down W boundary track just E of where it meets E–W track.

Site 6. 35°1′S, 141°45′E. (a) *Marsdenia.* Plot near SE corner of Lake Crosby, 0.2 km along Campground Track from its S end, on NE side of track. (b) *Rhyncharrhena.* Plot near S tip of Lake Kenyon, 0.5 km along Lake Kenyon Track from its W end.

APPENDIX 2

Seed sources used

a) The germination/seed age trial (all *Marsdenia*).
   1. 22 June 1976. Huckitta Station, Northern Territory.
   2. 30 October 1984. Railway and road reserve on W side of Calder Highway where it meets 22nd Street, about 4 km N of Red Cliffs.
   3. 22 October 1988. As for 2 above.
   4. 27 January 1990. Site 1 (Appendix 1).
b) The germination/temperature trial used no. 3 above and the seedling growth trial used no. 4. All *Rhyncharrhena* seeds used were collected at site 1 (Appendix 1) on 25 January 1990.

SPAWNING OF THE MOUNTAIN GALAXIAS, *GALAXIAS OLIDUS* GÜNTHER, IN BRUCES CREEK, VICTORIA

W. G. O'CONNOR AND J. D. KOEHN

Freshwater Ecology Branch, Department of Conservation and Environment,
123 Brown Street, Heidelberg, Victoria 3084

In Bruces Creek, Victoria, *Galaxias olidus* had a spawning season extending from early August to late October. Water temperatures ranged between 8° and 10.2°C over this period. Fertilized eggs were mainly found attached to the underside of boulders in riffles but some eggs were also found lodged amongst substrate or drifting downstream. *G. olidus* had a relatively low fecundity with an average of 198 eggs per female. Average egg diameter was 2.3 mm. All *G. olidus* were mature in their second year, although males matured earlier than females. The population had an overall sex ratio of 1:1 but the sexes were unevenly distributed, with more males in 0+ and more females in 2+ and 3+ year classes. The preferred habitat of adults was in pools. Fertilized eggs collected from the stream at an early stage of embryonic development hatched in the laboratory after 21 days at temperatures between 12.9° and 14.8°C. Newly hatched larvae averaged 9.4 mm in length.

THE MOUNTAIN GALAXIAS, *Galaxias olidus* Günther, a small (less than 145 mm long) native freshwater fish of the family Galaxiidae (McDowall 1980a), is generally found in small, headwater streams (Berra 1973, Fletcher 1979, Jackson 1981) at altitudes up to 1800 m (McDowall & Frankenberg 1981). The species occurs from southern Queensland to south-eastern South Australia (Merrick & Schmida 1984), although it has been recognized as having a highly fragmented distribution, often occurring in small isolated populations (Tilzey 1976, Cadwallader 1979, Jackson & Davies 1983, Cowden 1988).

G. olidus is widespread throughout Victoria (Cadwallader & Backhouse 1983), where its conservation status is "indeterminate" (Koehn & Morison 1990) due to uncertainty about the taxonomic status of the various taxa in this species complex. The population of this complex occurring in Bruces Creek conforms to the "typical" *G. olidus* form (see Cadwallader & Backhouse 1983). Although most of this taxon is common and widespread, *G. olidus* var. *fuscus* has been categorized as endangered in Victoria (Koehn & Morison 1990) and nationally (Jackson 1991).

Until recently there had been little investigation of the life history of *G. olidus* (Koehn & O'Connor 1990a). Most information remains unpublished in university theses (Harasymiw 1970, Fletcher 1979, Cowden 1988, Drayson 1989). The present paper contains information on the spawning of *G. olidus* in a small Victorian stream and includes data on habitat, population structure, sexual maturity, fecundity, spawning season and site, egg description, incubation period, and description of larvae.

STUDY SITE

The study was conducted in the upper reaches of Bruces Creek, Victoria, approximately 47 km north-east of Melbourne (Fig. 1), where McKenzie & O'Connor (1989) found a large population of *G. olidus*, the only fish species present. The absence of other species, particularly predatory species such as brown trout, *Salmo trutta*, was considered important as it allowed instream distribution and habitat preferences to be unaffected. *S. trutta* has been implicated in the displacement of *Galaxias olidus, G. truttaceus* and *G. brevipinnis* from preferred habitat areas (Koehn unpubl. data).

Bruces Creek rises on the western slopes of Mt Disappointment in the Great Dividing Range and flows firstly in a southwesterly then southeasterly direction to its confluence with the Plenty River. The study site was about 6.5 km downstream from the source of Bruces Creek at an altitude of 340 m. At the site, Bruces Creek is a small, shallow, third order stream with an average width of 2.0 m, an average depth of approximately 0.3, and consisting of alternating pools and riffles. The stream is in a relatively natural
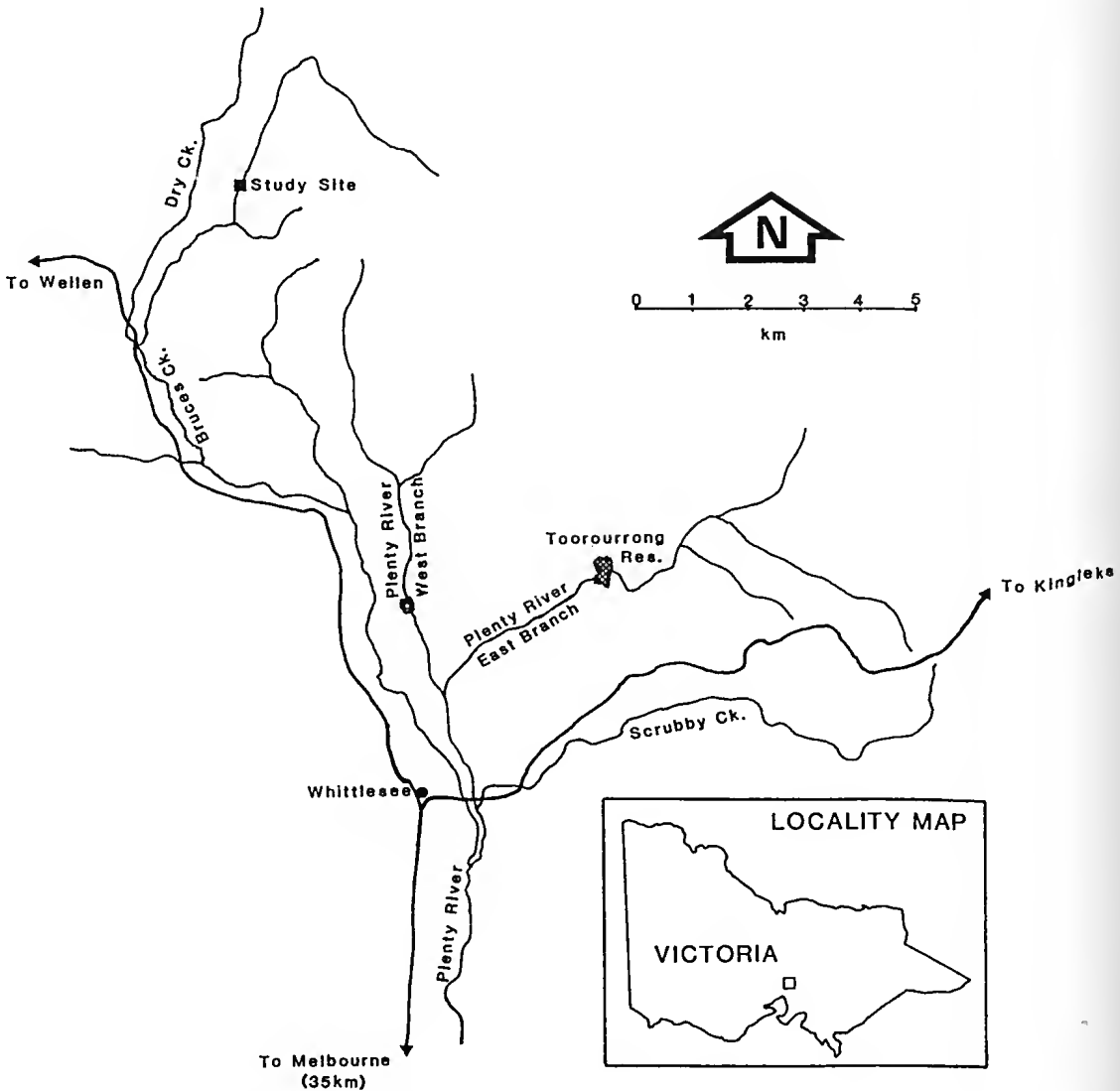
Fig. 1. Map showing the study site at Bruees Creek.

condition and contains abundant instream cover and wood debris.

Beardsell (pers. comm.) described the bank vegetation at the site as mountain grey gum riparian damp selerophyll forest (with no alien flora species) and the hillside vegetation as dry selerophyll. The surrounding land is State Forest.

METHODS

G. olidus was collected from Bruces Creek on 11 occasions between 15 August 1990 and 25 Octo-ber 1990 to examine spawning condition. This sampling period was selected as it coincided with previously reported spawning periods (Kochn & O'Connor 1990a). The length of stream fished for each sample ranged from 15 m to 60 m, and the number of fish collected in each sample varied from 22 to 62. Samples were taken over a 380 m stretch of stream, with only one section being sampled on each occasion. On 11 July 1991 an additional 24 ripe female fish were collected to determine egg numbers.

An estimate of the proportion of fish collected from pools and riffles was made during these

collections. On 4 October 1990 and 25 October 1990 sampling was conducted to determine population densities and on 11 July 1991 an additional 43 m stream section containing 5 pools and 4 riffles was sampled to determine pool or riffle preferences. Fish were captured from one electrofishing run, moving upstream using 2 operators, one with a dip net and polaroid glasses. Pools and riffles were separated by stop nets and the wetted perimeter of each section was measured and the area calculated. Fish numbers were adjusted using electrofisher efficiencies provided in Koehn & McKenzie (1985).

All fish sampling was conducted using a Smith Root Model 12 backpack electrofisher operated at settings of 120 Hz and 600 or 700 V. The length to caudal fork (LCF) of each fish was measured to the nearest mm and the spawning condition of each fish was assessed as per maturity stages in Pollard (1972).

Water temperature and conductivity were recorded during each sample using a Yellow Springs Model 33 Conductivity/Temperature meter. Relative water level was measured at a fixed depth gauge on each visit. The habitat at each spawning site was described. In determining pool or riffle preferences (11 July), stream length, width and depth were measured along with observations of the location of each fish collected. Water velocities were measured 100 mm above the substrate using an Ott mini-flow meter. Substrate particles were assessed visually, according to the size categories of Cummins (1962).

Fecundities were determined for 7 ripe females collected on 15, 22, 29 August 1990 and for 24 females collected on 11 July 1991 by dissecting gonads, prising eggs apart and counting individually.

Egg searches were carried out in both pools and riffles in the stream by the following methods:
(1) by inspecting instream habitat such as substrate and wood debris for attached eggs;
(2) by using drift nets of mouth opening 35 × 17 cm mesh mm (Hellawell 1986) positioned in the stream for (a) 3 hours and 22 hours where there had been no upstream disturbance of the streambed, and (b) several minutes, 0.5 to 2 m downstream from where substrate or instream cover had been gently disturbed (e.g. by lifting cobbles).

Collected samples were inspected visually for the presence of eggs. Diameters of 50 oocytes and of 28 fertilized eggs collected from the field, and lengths of 16 newly hatched larvae, were measured to the nearest 0.01 mm using a Nikon Profile model 6C-2 projector at a magnification of 10×.

Eggs collected in the field by the above methods were transferred to hatching baskets in the aquaria and the time taken to hatch was recorded. The hatching baskets consisted of 80 mm lengths of 90 mm diameter PVC pipe covered at one end with 0.5 mm nylon mesh netting. These baskets were suspended vertically in a 20 L aquarium tank with a through flow of approximately 27 L/h of filtered, dechlorinated water (aquarium water) (see Bacher & O'Brien 1989). Water temperatures were maintained between 12.3° and 14.9°C.

Sixty larvae hatched from collected eggs were placed in three 4 L tanks (20 per tank) filled with static, aerated aquarium water kept at ambient temperatures of 15.0°C to 17.2°C and the time taken to use up their yolk sacs observed.

The time to first feed was determined by placing 20 5-day-old larvae which had used their yolk sac in a tank to which 250 mL of water from a swamp containing abundant plankton was added. Larvae and water were then removed to a beaker twice daily and any feeding activity observed using a stereomicroscope. Guts were checked for food particles.

RESULTS

Habitat preferences

It was estimated that more than 90% of *G. olidus* collected in 1990 were from pools containing areas where water velocities were 0–0.15 m/sec, depths were 0.4–0.7 m, and there was abundant instream cover in the form of wood debris, submerged tree roots and undercut banks. The substrate of pools varied from predominantly silt/clay to boulder and cobbles. Sampling of 5 pools and 4 riffles on 11 July 1991 showed that 87% of *G. olidus* came from pools. Calculated on a per area basis, 85.5% of *G. olidus* occurred in pools and only 14.5% in riffles.

Two sections of the stream 22 m and 95 m long were electrofished on 4 October and 25 October 1990. Population densities of 1.09 and 0.84 fish/m² respectively were removed from one electrofishing run. Koehn & McKenzie (1985) recorded a 64% capture efficiency for common galaxias, *Galaxias maculatus*, from one electrofishing run using a Smith Root MKVIA electrofisher. These trials were conducted on a similar species, of similar size, under comparable conditions, with equipment considered to be of similar effi-

eieney. The population densities for *G. olidus* were thus adjusted by a faetor of 1.56 to give ealeulated population densities of 1.70 and 1.31 fish/m² respeetively.

Population structure

In the length–frequeney histogram for the *G. olidus* population (Fig. 2), four size elasses were reeognised (Table 1). Following Fletcher (1979) these size elasses wcre assigned estimated age classes of O+, 1+, 2+ and 3+ years, with O+ being assigned to juveniles from the 1989 spawning. In the 263 fish captured, the size ranged from 36 mm to 100 mm LCF, the largcst fish being ripe females.

Further analysis of the age elasses (Table 1) shows that the population was dominated by the 1+ age class, although the smaller O+ age class was likely to be under-represcnted due to less efficient sampling of smallcr fish (Koehn & McKenzie 1985). Only 2.3% of the population were 3 years or older, indieating that few fish live beyond their third year.

Details of sexual maturity for eaeh age-elass are given in Table 1. Most *G. olidus* do not reaeh sexual maturity in their first year (0+) when only 20% of male and 5% of female fish were sexually mature. The smallcst sexually mature male was 42 mm (LCF) and the smallcst female was 47 mm LCF. All fish were sexually mature by their second year (1+).

The overall sex ratio of mature fish in the population was 1 : 1 but the ratio of sexually mature individuals was not consistent through-out the age-classes. The earlier maturity of some O+ male fish increased thc apparent male : femalc ratio in that elass. Thc 1+ elass showed a 1.1 : 1 ratio whereas the 2+ class showed a 1 : 4.0 ratio. All six fish in the 3+ class were female.

Thc 31 ripe female *G. olidus* analysed for feeundity ranged betwecn 55 mm and 88 mm LCF (mean 66 mm) and eontained from 44 to 384 eggs (mean 198, N = 31, SE = 15). Number of eggs of *G. olidus* is positively eorrelated to fish length (r = 0.836, p < 0.01) (Fig. 3).

Spawning season

The spawning season for *G. olidus* in Bruces Creek in 1990 extended from early August to about late October. The percentage of spcnt fish in caeh sample increased from 10% to 93% during the study (Fig. 4). Although spawning had already begun by the start of the study, this sam-
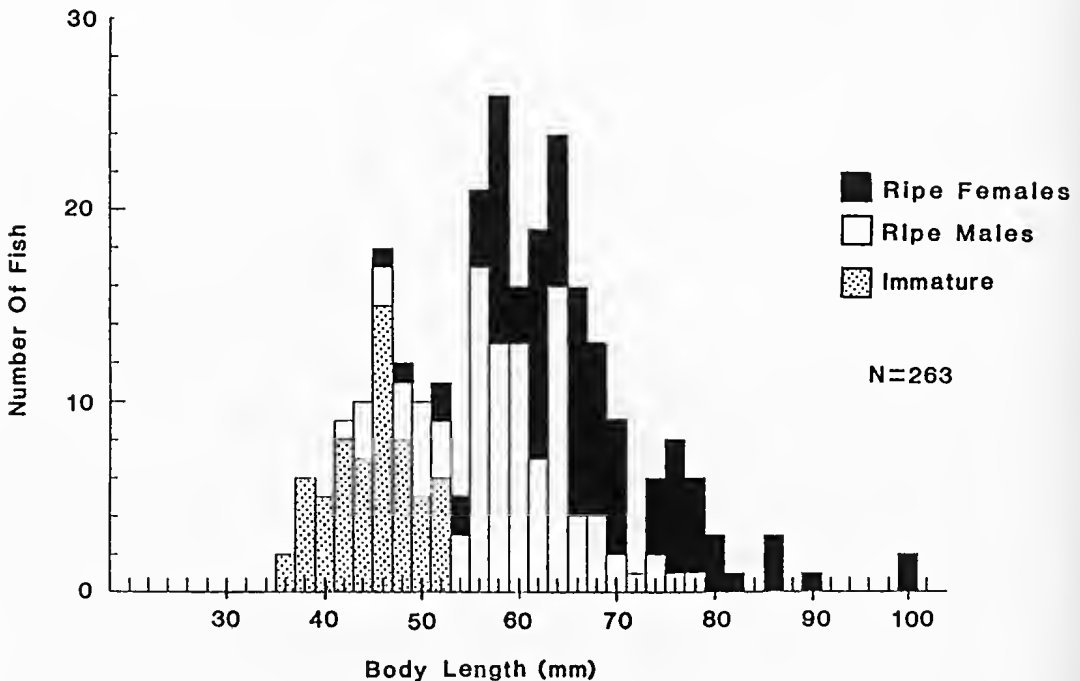

Fig. 2. Length–frequeney histogram for *Galaxias olidus* in Bruces Creek in 1990.

Age Class	Length Range (mm)	Fish Nos	% Popn	Ripe Males		Ripe Females		Immature Fish		Male: female ratio
				No.	%	No.	%	No.	%	
0+	36–52	83	31.6	17	20.5	4	4.8	62	74.7	4.1:1
1+	53–72	150	57.0	8.0	53.3	70	46.7	0	0	1.1:1
2+	73–82	24	9.1	4	16.7	20	83.3	0	0	1:4.0
3+	83–100	6	2.3	0	0	6	100	0	0	N/A
Total		263		101		100		62		1.0:1

Table 1. Length range, number of fish collected, percentages of ripe males, females and immature fish, and sex ratios for each age class of the *Galaxias olidus* population during the 1990 spawning season in Bruces Creek.
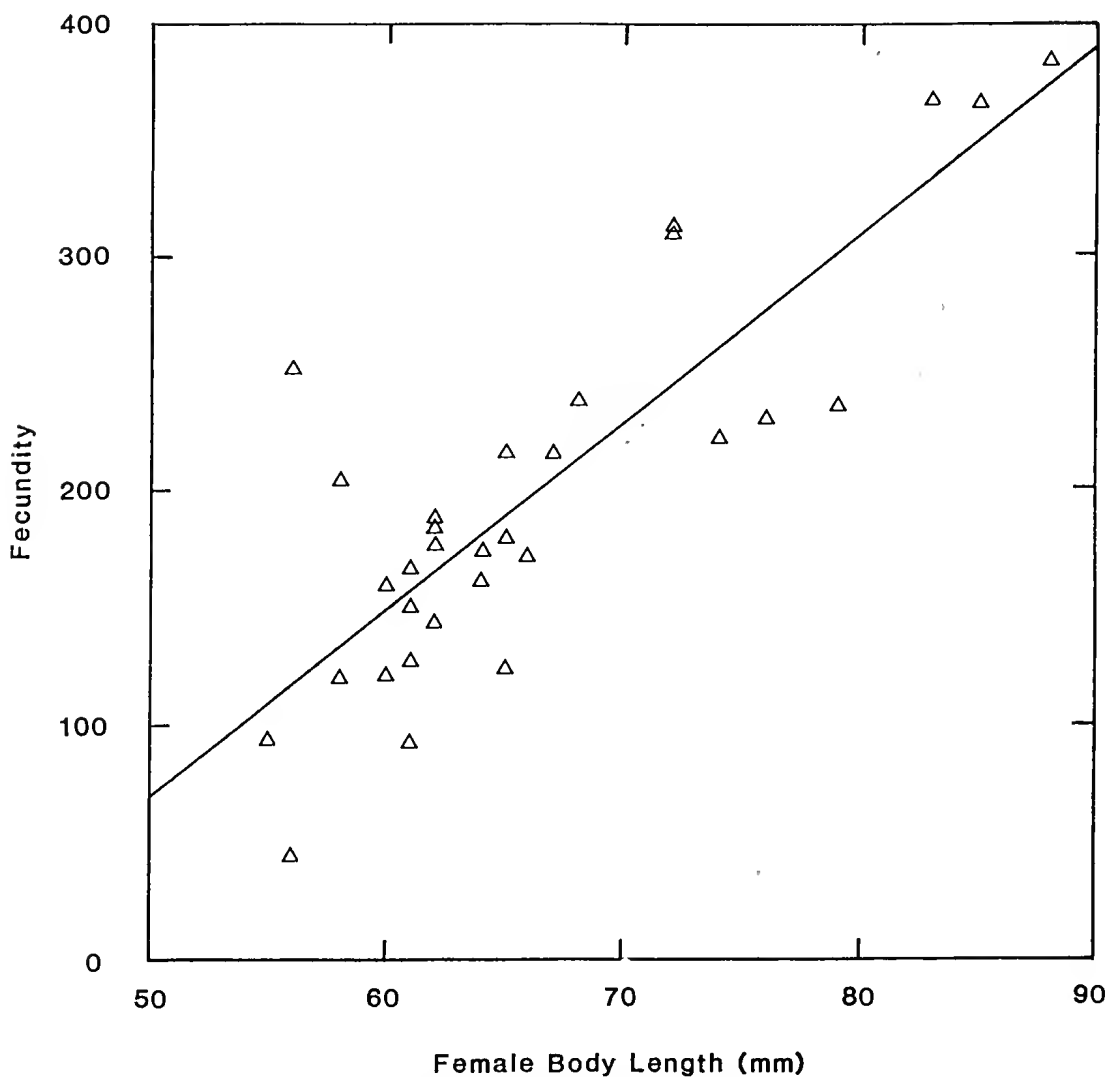

Fig. 3. Relationship between length and fecundity for *Galaxias olidus* females in Bruces Creek.
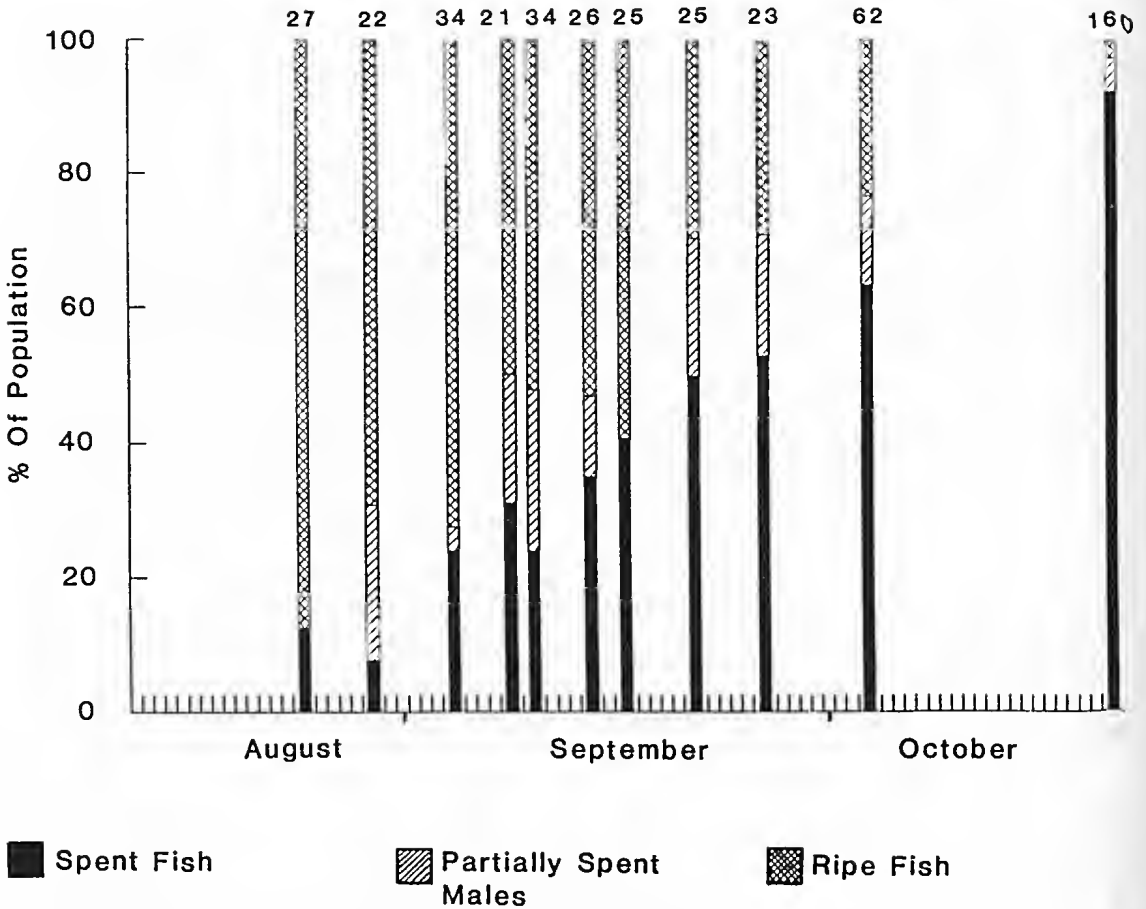
Fig. 4. Percentage of ripe and spent *Galaxias olidus* during the 1990 spawning season in Bruces Creek. Numbers of fish examined are given above each column.

pling period covered most of the spawning season.

Most females collected were either ripe or spent, only two being part spent, an indication that females lay all their eggs at once. Both part spent females had red bruising on their sides and abdomen suggesting they may have been in the act of spawning when captured. Several other females (spent and running ripe) and males (part spent) had similar marks.

Eggs in some gravid females in the 4 October sample and in all gravid females in the 25 October 1990 sample were noticed to be smaller in size, possibly indicating that a small percentage of females did not spawn and were undergoing involution. Throughout the breeding season a proportion of males were partially spent, suggesting that each male may be involved in more than one fertilization.

Daytime water temperatures between 15 August 1990 and 4 October 1990 were between 8.0° and 10.2°C and water levels rose to a maximum recorded level of 70 mm above the normal watermark, although observations indicated that higher short-term levels did occur. Water temperature was 13.5°C on 25 October 1990. Water conductivities varied from 73 to 90 EC units.

Spawning sites

Four individual spawning sites were found; three were at the downstream end of a riffle at the head of a pool containing large numbers of ripe fish, and one was at the head of a riffle immediately downstream of a pool. No fish were collected from the near vicinity of any of the spawning sites.

Eggs were found adhering strongly to the underside of boulders larger than 180 mm in diameter situated in riffles immediately upstream and downstream of pools. Eggs were not found attached to wood debris or other instream objects.

The underside of each boulder was relatively flat but slightly raised (up to 60 mm) from the streambed so that the eggs were sheltered from the main water current. Water velocities in the riffles around the boulders ranged from approximately 0.2 to 0.5 m/sec. On two boulders which had not been disturbed 179 eggs and 26 eggs were counted. Eggs were attached either singly or in groups of 6 to 62; the eggs were usually one and not more than two layers thick and were coated with sand and gravel particles. The boulder with 179 eggs contained eggs at three different stages of embryological development.

In four drift nets set for 3 hours below undisturbed sites only one egg was collected. A repeat set of that net 2 days later at the same site collected one more egg. The net had been positioned in the main gently flowing current (0.1 m/sec) about 1.5 m downstream of a riffle. No eggs were collected in two nets set overnight for 22 hours.

When substrate or instream objects such as wood debris were disturbed by gentle lifting two eggs were caught in one drift net and nine in another held immediately downstream of two riffles. The substrate of these two riffles comprised boulder 10%, cobble 40%, pebble 30% and gravel 20%. One egg was collected from a pool with a "flat" streambed whose substrate comprised sand/silt 70%, boulder 10%, and cobble 10%. No eggs were found in four other pools and three other riffles "searched" in the same manner.

We surmise that most eggs of *G. olidus* are attached to the underside of boulders, but some eggs come to rest in the substrate and a few drift downstream.

Egg description and incubation period

Unfertilised oocytes were spherical, demersal, white or opaque and adhesive. Fertilized, water hardened eggs were spherical, demersal, transparent and initially adhesive but single, unattached eggs became progressively less adhesive.

The diameters of oocytes and fertilized eggs at the earliest stages of development and at the "eyed" stage were:

Mean oocyte diameter = 2.29 mm (N = 50, SE = 0.22 mm)
Mean egg (early stage) diameter = 2.4 mm (N = 8, SE = 0.11 mm)
Mean egg (eyed) diameter = 2.29 mm (N = 20, SE = 0.20mm).

Three eggs collected on 5 September 1990 were at the earliest stage of embryological development (i.e. no embryo in nucleus) and took 21 days to hatch at temperatures of 12.9–14.8°C. All other viable eggs collected were at later stages of development and hatching times were 9–14 days at 14.0–15.0°C.

Larvae

The lengths of larvae measured 0–6 hours after hatching ranged from 9.0 mm to 9.8 mm TL. Mean length was 9.39 mm (N = 16, SD = 0.26). The larvae had small yolk sacs 1.4 mm long. In the light, these larvae were active swimmers throughout the water column including at the surface, but they also lay motionless on the bottom of the tank for several minutes. Larvae appeared to have absorbed their yolk sacs after 5 days and commenced feeding 3 days later.

DISCUSSION

Our study provided information on *G. olidus* from relatively natural surroundings unaffected by major habitat alterations or by other fish species including introduced predators. The major habitat preference of *G. olidus* in Bruces Creek was clearly for pool areas with slow-flowing, deeper water in a stream containing abundant instream habitat of wood debris, submerged tree roots and undercut banks and intact riparian vegetation. Such attributes in streams have been recognised as important for freshwater fishes (Cadwallader & Backhouse 1983, OCE 1988, Lloyd & Walker 1988, Koehn & O'Connor 1990a, 1990b). Riparian vegetation prevents erosion, provides instream habitat and shading, as well as terrestrial invertebrates which form an important element in the diet of *G. olidus* (Cadwallader et al. 1980). McDowall (1980b) has suggested that removal of riparian vegetation correlates with the reduction in population numbers of several galaxias species in New Zealand.

The relatively high population densities of *G. olidus* (1.31–1.70 fish/m^2) in Bruces Creek are comparable to those of 0.79 and 2.83 fish/m^2 reported by Fletcher (1979) in Watchbox Creek and at Mt Buffalo. Tilzey (1976) reported den-

sitics of up to 3.7 fish/m² in tributaries of Lake Eucumbene. Such densities are likely to be attributable to the presence of high-quality habitat and the absence of brown trout, *Salmo trutta*. The effects of *S. trutta* on the abundance and distribution of *G. olidus* have been comprehensively documented, with mutually exclusive populations often occurring and a fragmentation of the range of *G. olidus* resulting in isolated populations often being reported (Tilzey 1976, Cadwallader 1979, Fletcher 1979, Jackson & Davies 1983, Cowden 1988, Jones et al. 1990, Lintermans & Rutzou 1990).

After using otoliths to age *G. olidus*, Cowden (1988) concluded that most individuals did not reach maturity until their third year (age 2+). Drayson (1989), however, examined otoliths from *G. olidus* collected in the same catchment as Cowden and considered their annular patterns to be uneven and therefore unsuitable as a means of accurately aging this species. From the length frequency distribution (Fig. 2), we suggest estimated age classes O+ (1st year), 1+ (2nd year), 2+ (3rd year) and 3+ (4th year) based on a similar population structure reported by Fletcher (1979). These three age classes make up almost the entire population (97%) of *G. olidus* in Bruces Creek. Most *G. olidus* did not mature in their first year but all were mature by their second year. These results are consistent with those of Fletcher (1979), namely that maturity is mostly reached at age (1+) and that the maximum age is probably 4 years.

Although the sex ratio for sexually mature fish is 1:1, the ratio is not consistent throughout the age classes. Males mature earlier than females but appear to have a higher mortality; consequently females predominate in the 2+ and 3+ age classes. Cowden (1988) also reported a 1:1 sex ratio.

The fecundity of *G. olidus* is one of the lowest among galaxias species in Australia. A mean fecundity of 198 found in this study is similar to the value of 243 recorded by Cowden (1988). Of Victorian galaxiid species, only *Galaxiella pusilla*, a wholly freshwater species, has a similar fecundity (generally 100–200; Humphries 1986). Fecundities of diadromous galaxiid species are generally much higher: common galaxias, *Galaxias maculatus*, up to 13,500 (McDowall 1968); spotted galaxias, *G. truttaceus*, up to 16,000 (Humphries 1989); and broad-finned galaxias, *G. brevipinnis*, up to 23,000 (Koehn and O'Connor unpubl. data).

The breeding season of *G. olidus* has been variously reported as winter through to summer (Cadwallader & Backhouse 1983). *G. olidus* spawns in October in Victorian alpine streams (Fletcher 1979); from early August to early September in the Australian Capital Territory; and during late August to early September in southern Queensland (Marshall 1989). The variation in onset of these spawning seasons may be due to the corresponding differences in water temperatures. Cowden (1988) recorded temperatures of 6.5–8.2°C, whereas Marshall (1989) estimated a temperature range of about 15–20°C. In Bruces Creek the main breeding season extended for over 2 months from early August to about mid October, when the temperature range was 8.0–10.2°C.

G. olidus employed a spawning strategy indicative of a fish species that has a low fecundity and needs to maximise the survival of eggs and larvae. This strategy involves laying a small number (average fecundity of 198) of relatively large (2.3 mm) adhesive eggs in a protected site, usually a boulder more than 180 mm in diameter and with a narrow gap between the underside of the boulder and the streambed. Similar spawning sites for *G. olidus* have been reported by Cowden (1988). In Bruces Creek the eggs were attached to the underside of the boulders where they may be protected from possible predators (especially fish), disturbance, strong water currents and possible smothering by sediment. All the boulders were in riffles where the surrounding water was relatively fast-flowing (0.2–0.5 m/sec) and well oxygenated. Eggs were not found attached to any other instream objects such as wood debris.

Red bruising on the abdomen and sides of many spawning fish of both sexes suggests that the fish rubbed against hard objects during spawning. Bruising is highly likely in enclosed locations where the fish would probably have to press hard against the underside of boulders in a lateral or upside down position to deposit eggs and milt.

A least three different stages of embryonic development were recorded for eggs at one spawning site. Because females appear to lay all their eggs at once, it appears that more than one spawning may take place at a suitable site. The strategy of laying a small number of relatively large, adhesive eggs at an enclosed site has been described for another Victorian freshwater fish, the freshwater blackfish, *Gadopsis marmoratus* (Jackson 1978). *G. marmoratus* attaches its eggs to the inside of hollow logs which are then guarded by an aggressive male fish (Koehn unpubl. data). Parental care of eggs appears un-

likely for *G. olidus* as relatively few fish were collected from the riffle areas and there was no evidence of eggs being guarded. We surmise that ripe males and females from the pools move into the riffles to spawn, then return to their preferred habitat. The collection of eggs in drift nets from both disturbed and undisturbed sites indicates that not all eggs are attached to the spawning site. Such "free" eggs may originate in three ways.

1. Eggs not becoming successfully attached to the spawning site during spawning. This may be expected when fish are attempting to attach and fertilise eggs on the underside of a boulder. There appears to be a large discrepancy between female fecundities and the number of eggs found attached to boulders, suggesting that not all eggs become attached.

2. Eggs being laid at less sheltered sites in the stream where attachment does not occur or where the eggs may easily be displaced. There is, however, no evidence for such sites.

3. Eggs being dislodged from the spawning boulder. This appears unlikely as the eggs adhere strongly to the rock and to each other. Some dislodgement may be possible, however, if subsequent spawning activity occurs at the same site.

The collection of single, non-adhesive, developing eggs at undisturbed sites suggests that some eggs may be carried downstream either by drifting in the current or by rolling along the streambed. Such a mechanism would aid downstream dispersal. *G. olidus* eggs are initially very adhesive, but those at a later stage of development that were unattached were non-adhesive. Some of these eggs probably lodge in the interstices of the substrate in riffles or settle to the streambed in pools. Such eggs were collected by disturbing the substrate.

Hence, the eggs of *G. olidus* may be found in three situations: (a) attached, (b) lodged in the substrate, or (c) drifting. Each of these situations involves a different degree of disturbance to the egg itself, possibly leading to variations in hatching times. Cowden (1988) found that hatching of eggs could be induced by gently swirling the water in which they were held. The induced hatching of eggs of *G. truttaceus* and *G. brevipinnis* by disturbance has also been noticed (Koehn & O'Connor unpubl. data). Cowden (1988) recorded, however, that "induced" fry were smaller and less active than normal.

Exact hatching times were not obtained, but fertilized eggs collected in the stream at an early embryonic stage took 21 days to hatch at temperatures of 12.9° to 14.8°C. Using Cowden's (1988) results, hatching times were estimated to be 47 days at about 9°C and 32 days at about 13°C. Average temperatures in Bruces Creek from August to mid October were about 9°C, while temperatures in late October were about 13°C. Assuming hatching is temperature dependent, these figures suggest that hatchings in Bruces Creek probably occurred from early October until mid December.

Newly hatched larvae emerged at 9.4 mm TL with relatively small yolk sacs which were fully absorbed after about 5 days, with feeding commencing after a further 3 days. Large, well developed larvae with small yolk sacs are more mobile, able to seek shelter and hence less vulnerable than smaller fry with large yolk sacs. This is consistent with the spawning strategy we have described for *G. olidus*.

Increased sediment input into streams has been recognised as having adverse effects on Victorian native freshwater fish (Cadwallader & Backhouse 1983, OCE 1988, Mitchell 1990, Koehn & O'Connor 1990a, 1990b). Sedimentation would be likely to fill or cover potential spawning sites, and the availability of sites under boulders appears essential for spawning. If such sites were not available or were heavily silted so that eggs do not adhere, spawning may not occur or may have reduced success. Likewise, the loss of interstitial spaces in the substrate due to sedimentation may cause increased mortalities to unattached eggs which normally become lodged there. Eggs of *Gadopsis marmoratus, Galaxias truttaceus* and *G. brevipinnis* have shown high mortalities when covered with light layers of silt (Koehn & O'Connor unpubl. data).

Sedimentation and the well-documented threat of predation by introduced species are likely to be major environmental threats to *G. olidus* in otherwise natural streams.

ACKNOWLEDGEMENTS

Silviculture Systems Project funded by the Department of Conservation and Environment.

REFERENCES

BACHER, G. J. & O'BRIEN, T. A., 1989. Salinity tolerance of the eggs and larvae of the Australian grayling *Prototroctes maraena* Günther (Salmoniformes: Prototroctidae). *Australian Journal of Marine and Freshwater Research* 40: 227–230.

BERRA, T. M., 1973. A home range study of *Galaxias bongbong* in Australia. *Copeia* 1973: 363–366.

CADWALLADER, P. L., 1979. Distribution of native and introduced fish in the Seven Creeks River system, Victoria. *Australian Journal of Ecology* 4 : 361–385.

CADWALLADER, P. L. & BACKHOUSE, G. N., 1983. *A Guide to the Freshwater Fish of Victoria.* Victorian Government Printer, Melbourne, 249 p.

CADWALLADER, P. L., EDEN, A. K. & HOOK, R. A., 1980. Role of streamside vegetation as a food source for *Galaxias olidus* Günther (Pisces: Galaxiidae). *Australian Journal of Marine and Freshwater Research* 31: 257–262.

COWDEN, K. L. B., 1988. Aspects of biology of the mountain galaxiid, *Galaxias olidus* Günther (Pisces: Galaxiidae), in Pierces Creek, ACT. BSc (Hons) thesis, Department of Zoology , Australian National University, Canberra.

CUMMINS, K. W., 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lentic waters. *American Midland Naturalist* 67: 477–504.

DRAYSON, N., 1989. Aspects of the biology and population structure of the mountain galaxias, *Galaxias olidus*, in the ACT. BSc (Hons) thesis, Department of Zoology, Australian National University, Canberra.

FLETCHER, A. R., 1979. Effects of *Salmo trutta* on *Galaxias olidus* and macroinvertebrates in stream communities. MSc thesis, Department of Zoology, Monash University, Clayton, Victoria.

HARASYMIW, B. J., 1970. Some aspects of the schooling behaviour of *Galaxias bongbong*. BSc (Hons) thesis, Department of Zoology, Australian National University, Canberra.

HELLAWELL, J. M., 1986. *Biological Indicators of Freshwater Pollution and Environmental Management.* Elsevier Applied Science Publishers, Barking, Essex, England.

HUMPHRIES, P., 1986. Observations on the ecology of *Galaxiella pusilla* (Mack) (Salmoniformes: Galaxiidae) in Diamond Creek, Victoria. *Proceedings of the Royal Society of Victoria* 98: 133–137.

HUMPHRIES, P., 1989. Variation in the life history of diadromous and landlocked populations of the spotted galaxias, *Galaxias truttaceus* Valen-

ciennes, in Tasmania. *Australian Journal of Marine and Freshwater Research* 40: 501–518.

JACKSON, P. D., 1978. Spawning and early development of the river blackfish, *Gadopsis marmoratus* Richardson (Gadopsiformes: Gadopsidae), in the McKenzie River, Victoria. *Australian Journal of Marine and Freshwater Research* 29: 293–298.

JACKSON, P. D., 1981. Trout introduced into southeastern Australia: their interaction with native fishes. *Victorian Naturalist* 98: 18–24.

JACKSON, P. D., 1991. Australian threatened fishes – 1990 supplement. *Australian Society for Fish Biology Newsletter* 21: 11–13.

JACKSON, P. D. & DAVIES, J. N., 1983. Survey of the fish fauna in the Grampians region, southwestern Victoria. *Proceedings of the Royal Society of Victoria* 95: 39–51.

JONES, H. A., RUTZOU, T. & KUKOLIC, K., 1990. *Distribution and Relative Abundance of Fish in the Naas–Gudgenby Catchment.* Research Report No. 3, Australian Capital Territory Parks and Conservation Service, Canberra.

KOEHN, J. D. & McKENZIE, J. A., 1985. *Comparison of Electrofisher Efficiencies.* Arthur Rylah Institute for Environmental Research, Technical Report Series No. 27, Department of Conservation and Environment, Victoria.

KOEHN, J. D. & MORISON, A. K., 1990. A review of the conservation status of native freshwater fish in Victoria. *Victorian Naturalist* 107: 13–25.

KOEHN, J. D. & O'CONNOR, W. G., 1990a. *Biological Information for Management of Native Freshwater Fish in Victoria.* Victorian Government Printer, Melbourne, 165 pp.

KOEHN, J. D. & O'CONNOR, W. G., 1990b. Threats to Victorian native freshwater fish. *Victorian Naturalist* 107: 5–12.

LLOYD, L. N. & WALKER, K. F., 1988. Management of snags (wood debris) and river floodplain vegetation for native fish in the Murray–Darling River system. In *Proceedings of the Workshop on Native Fish Management, Canberra, 16–17 June 1988*, Murray–Darling Basin Commission, Canberra, 99.

LINTERMANS, M. & RUTZOU, T., 1990. *The Fish Fauna of the Upper Cotter River Catchment.* Research Report No. 4, Australian Capital Territory Parks and Conservation Service, Canberra.

MARSHALL, J., 1989. *Galaxias olidus* in southern Queensland. *Fishes of Sahul* 5: 223–225.

McDOWALL, R. M., 1968. *Galaxias maculatus* (Jenyns), the New Zealand whitebait. *New Zealand Marine Department of Fisheries Research Division, Fisheries Research Bulletin* (new series) 2: 1–84.

McDOWALL, R.M., 1980a. Family Galaxiidae. Galaxiids. In *Freshwater Fishes of South-Eastern Australia*, R. M. McDowall, ed, Reed Books, Sydney, 55–69.

McDOWALL, R. M., 1980b. Forest cover over streams

is vital to some native freshwater fishes. *Fish and Bird* 13: 22–24.

McDowall, R. M. & Frankenberg, R. S., 1981. The galaxiid fishes of Australia. *Records of the Australian Museum* 33: 443–605.

McKenzie, J. A. & O'Connor, W. G., 1989. *The Fish Fauna and Habitats of the Plenty River.* Arthur Rylah Institute for Environmental Research, Technical Report Series No. 96, Department of Conservation and Environment, Victoria.

Merrick, J. R. & Schmida, E. G., 1984. *Australian Freshwater Fishes.* Griffin Press, Netley, South Australia, 409 p.

Mitchell, P. A., 1990. *The Environmental Condition of Victorian Streams.* Department of Water Resources, Melbourne, 102 p.

OCE (Officer of the Commissioner for the Environment), 1988. Physical modification to rivers and streams. In *State of the Environment Report 1988,* Victorian Government Printer, Melbourne, 168–176.

Pollard, D. A., 1972. The biology of the landlocked form of the normally catadromous salmoniform fish *Galaxias maculatus* (Jenyns). 3. Structure of the gonads. *Australian Journal of Marine and Freshwater Research* 23: 17–38.

Tilzey, R. D. J., 1976. Observations on interactions between indigenous Galaxiidae and introduced Salmonidae in the Lake Eucumbene catchment, NSW. *Australian Journal of Marine and Freshwater Research* 27: 551–564.

SYMPOSIA

Papers presented at Regional and other Symposia organized by the Royal Society of Victoria, as well as special publications which have been published in the *Proceedings*, are available as follows:

THE VICTORIAN HIGH PLAINS. Included in Vol. 75, Part 2, 1962. $8.25 per copy.

UPPER MESOZOIC MICROFLORAS FROM S.E. AUSTRALIA by Mary E. Dettman. Reprinted from Vol. 77, Part 1, 1963. $25.00 per copy.

THE VICTORIAN MALLEE. Included in Vol. 79, Part 2, 1966. $8.25 per copy.

EAST GIPPSLAND SYMPOSIUM. Vol. 82, Part 1, 1969. $7.00 per copy.

THE AQUATIC ENVIRONMENT AND MAN. Included in Vol. 83, Part 1, 1970. $7.00 per copy.

WEST GIPPSLAND SYMPOSIUM. Reprinted from Vol. 84, Part 1, 1971. $2.80 per copy.

BIBLIOGRAPHY OF BASS STRAIT 1797–1971. Included in Vol. 85, Part 2, 1973. $2.50 per copy.

THE URBAN ENVIRONMENT AND LIFE. Reprinted from Vol. 86, Part 2, 1974. $4.00 per copy.

THE WESTERNPORT BAY SYMPOSIUM. Reprinted from Vol. 87, Part 1, 1975. With large map in separate pocket. Morphology of Westernport Bay 1:50,000. $6.00 per copy.

THE OTWAY REGION SYMPOSIUM. Reprinted from Vol. 89, Part 1, 1977. $8.00 per copy.

THE MURRAY-DARLING RIVER SYSTEM. Reprinted from Vol. 90, Part 2, 2978. $16.00 per copy.

VICTORIA'S COAST AND CONTINENTAL SHELF. Reprinted from Vol. 92, Parts 1 & 2, 1981. $25.00 per copy.

MANAGEMENT OF SCIENCES SYMPOSIUM. Reprinted from Vol. 97, Part 2, 1985. $4.00 per copy.

Payment, in Australian dollars, must accompany all orders. Prices include postage (surface mail) and handling charges. All orders should be sent to:

The Executive Officer,
Royal Society of Victoria,
9 Victoria Street,
Melbourne, Victoria 3000
Australia

TAXONOMY AND DISTRIBUTION OF THE AUSTRALIAN TIGER SNAKES (*NOTECHIS*) AND COPPERHEADS (*AUSTRELAPS*) (SERPENTES, ELAPIDAE)

P. A. RAWLINSON
(Deceased April 1991)

Department of Zoology, La Trobe University, Bundoora, Victoria 3083
Reprint requests to: A. J. Coventry, Museum of Victoria, 328 Swanston Street, Melbourne, Victoria 3000

RAWLINSON, P. A., 1991:12:31. The taxonomy of the Australian tiger snakes (*Notechis*) and copperheads (*Austrelaps*) (Serpentes, Elapidae). *Proceedings of the Royal Society of Victoria* 103 (2): 125–135. ISSN 0035-9211.

The taxonomic histories of species of the Australian snake genera *Notechis* and *Austrelaps* are reviewed. A lectotype is selected for *Hoplocephalus superbus* Günther, 1858 (type species of *Austrelaps*) and neotypes are proposed for the following species: *Alecto fasciolatus* Jan & Sordelli, 1873; *Alecto labialis* Jan, 1859; *Hoplocephalus fuscus* Steindachner, 1867; *Hoplocephalus ramsayi* Krefft, 1864; and *Naja (Hamadryas) scutata* Peters, 1861 (type species of *Notechis*). *Hoplocephalus bransbyi* Macleay, 1878 is a junior objective synonym of *H. ramsayi*. *Hoplocephalus fuscus* and *Alecto fasciolatus* are objective synonyms of each other and junior subjective synonyms of *Hoplocephalus ater*. *Austrelaps labialis* and *Austrelaps ramsayi* are formally removed from the synonymy of *Austelaps superbus* and given full specific status.

THE SYSTEMATICS of Australian reptiles were poorly understood until recent times. A number of historical problems had contributed to this situation, often including many of the following: (1) type specimens lost or not allocated; (2) type specimens inaccurately or inadequately described; (3) type localities not given, too general or inaccurate; (4) early synonyms overlooked or more recent synonyms not quoted; (5) insufficient attention given to the variability of a species over its whole range; (6) lack of accurate data on morphology and biology, many authors simply repeating earlier accounts; and (7) generic changes of species without re-examination of type specimens.

The publication by Cogger et al. (1983) of a comprehensive catalogue of the Australian herpetofauna rectified many taxonomic errors and clarified the status of most taxa, but several nomenclatural problems remained unresolved. The present paper deals with two such problem taxa, the Australian tiger snakes (*Notechis* spp.) and copperheads (*Austrelaps* spp.).

Abbreviated prefixes of specimen numbers cited herein refer to the following institutions: Australian Museum, Sydney (AM); Natural History Museum, London (BMNH); Museum of Victoria, Melbourne (NMV); South Australian Museum, Adelaide (SAM); Zoologisches Museum, Museum für Naturkunde der Humboldt Universität zu Berlin (ZMB); Zoologisches Museum, Universität Hamburg (ZMH)

SYSTEMATICS

Austrelaps Worrell, 1963a

Type species. Hoplocephalus superbus Günther, 1858.

Remarks. Austrelaps was established for the two species *Hoplocephalus superbus* and *Alecto signata* Jan, 1859, but the latter is now assigned to *Hemiaspis* Fitzinger, 1860 (Cogger et al. 1983). The species *superbus* (first as *Denisonia superba* and later as *Austrelaps superbus)* has been recognised by all authors since Boulenger (1896), but Rawlinson (1969, 1971) stated that forms assigned to the species include two distinct morphological groups differing in distribution and ecology. These groups were referred to as the lowlands and highlands forms. A third group from the Mount Lofty Ranges and Kangaroo Island, South Australia, originally regarded by Rawlinson (1969) as an isolate of the highlands form, was recognised by Sutherland (1983) as the Adelaide Hills or pigmy copperhead. This group is referred to herein as the dwarf form. Shine (1987a) stated that the lowlands, highlands and dwarf forms correspond respectively to *A. superbus, A. ramsayi* (Krefft, 1864) and *A. labialis* (Jan, 1859). This view has been confirmed in the present study by examination of existing types and reference to original descriptions and illustrations.

Austrelaps superbus and *A. ramsayi* occupy similar habitats in southeastern Australia but *A. ramsayi* is restricted to higher altitudes and more northerly areas (Fig. 1). The distributions of the two species interdigitate and abut in eastern Victoria, particularly in the area south and west of the Baw Baw Plateau, but the species have not been collected syntopically. *Austrelaps labialis* is known only from two disjunct areas, Kangaroo Island where it is widespread, and the Adelaide Hills roughly within the 1000 mm isohyet.

Key to species of *Austrelaps*

1.	Supralabials boldly marked, anteroventral quarter cream, remainder dark brown, the two colours meeting at a sharp diagonal demarcation; lower anterior temporal usually in point contact with or failing to contact lower postocular 2
—	Supralabials with weakly defined, narrow whitish anterior margins; lower anterior temporal usually in broad contact with lower postocular; ventrals 143–164 . . . . *Austrelaps superbus*
2.	Ventrals 150 or more; eastern Victoria to New England region of New South Wales . . . . *Austrelaps ramsayi*
—	Ventrals 148 or fewer; Kangaroo Island and high rainfall areas in the Mt Lofty Ranges, South Australia . . . . *Austrelaps labialis*

Austrelaps superbus (Günther, 1858)

Alecto curta.—Duméril et al. 1854: 1252–1254 (in part; non *Naja curta* Schlegel, 1837).

Hoplocephalus superbus Günther 1858: 181.

Alecto schmidti Jan & Sordelli 1873: liv. 44, pl 1, fig. 4.

Denisonia superba.—Boulenger 1896: 353 (in part).

Austrelaps superbus.—Worrell 1963: 3 (in part).—Sutherland 1983: 50–52.—Cogger et al. 1983: 218 (in part).

Notechis superbus.—Storr 1982: 235 (in part).

Remarks. Günther (1858) described *Hoplocephalus superbus* on the basis of 15 specimens in the Natural History Museum, London. Six of these were later used by Günther (1863) to erect a new species, *Hoplocephalus minor*, subsequently referred to the new genus *Elapognathus* by Boulenger (1896); one of these six specimens was apparently exchanged to the Zoologisches Museum in Berlin (ZMB 4298) and is presumed lost. The remaining nine syntypes of *H. superbus* have been examined by the author (see Appendix 1) and all are referrable to the lowlands form of *superbus*, to which form the species name is here restricted. Several of the syntypes are in poor condition, being soft and with peeling epidermis or damage to the head. The best preserved, BMNH 1946.1.20.37, from "Tasmania" (R. Gunn), is hereby designated the lectotype of *H. superbus*.

Alecto schmidti Jan & Sordelli (1873, liv. 44, pl. 1, fig. 4) is in colour pattern and proportions a specimen of *Austrelaps superbus* as that species is recognised here. The holotype (ZMH 478), which has been examined by the author, is in poor condition and bleached, and locality information accompanying it is limited to "1877 Australia".

Austrelaps labialis (Jan, 1859)

Alecto labialis Jan 1859a: 128.

Denisonia superba.—Boulenger 1896: 353 (in part).

Austrelaps superbus.—Cogger et al. 1983: 218 (in part).

Austrelaps labialis.—Shine 1987a: 22.

Remarks. The history of the name *Alecto labialis* has been discussed in part by Coventry & Rawlinson (1980). The species was stated by Jan (1863) to be based on a specimen from New Holland in the Zoologisches Museum at Göttingen, but unsuccessful searches of the collections there by the author and by others suggest that the holotype is lost. No illustration accompanied the initial description (Jan 1859a) but a reprint issued as a separate in the same year (Jan 1859b) included plates with illustrations of the type. Confusion arose when Jan & Sordelli (1873, liv. 44, pl. 1, fig. 1) depicted as *A. labialis* a specimen of a species now known as *Drysdalia coronoides* (Günther, 1858) (see Coventry & Rawlinson 1980).

The illustrations of *A. labialis* given by Jan (1859b) clearly show the boldly diagonally barred labials (described as "half yellow, half black"; see Appendix 2) and the lower anterior temporal well separated from the lower postocu-

lar, both features characteristic of the highlands and dwarf forms of the copperhead but not of the lowlands form. The dwarf form is shorter-bodied than the highlands form, having 135–148 ventrals (mean 141, n = 30; one specimen with 157), whereas the highlands form has ventral counts of 150–160 (mean 156.8, n = 30). The ventral count of 136 reported by Jan (1859) for *A. labialis* could therefore apply only to the dwarf form. Thus, in the absence of any other available name, the correct name for the dwarf form is *Austrelaps labialis* (Jan, 1859).

In order to stabilise the name, specimen SAM R26414, a female, from Islet 477, Pelican Lagoon, Kangaroo Island, South Australia, is here designated as neotype. The neotype has the following taxonomically significant features. Midbody scale rows 15. Ventrals 139. Anal single. Subcaudals 43, entire, excepting the last three which are divided. Lower anterior temporal well separated from lower of two postoculars on each side. Supralabials 6/6. Colour very dark brown dorsally, the lateralmost scales grey-white with a dark trailing edge, the size and contrast of the pale area decreasing posteriorly and becoming uniformly dark by midbody. Venter
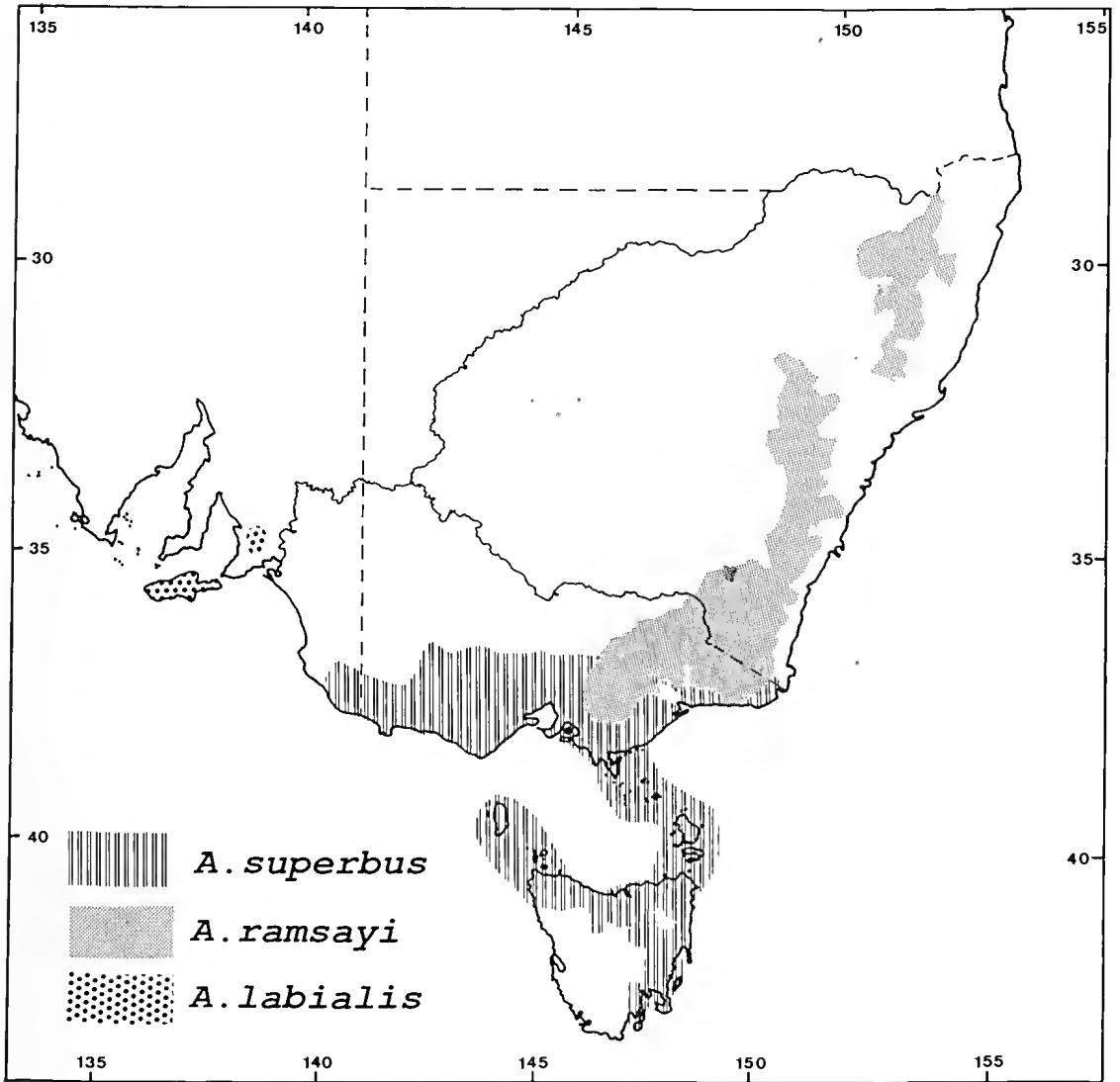

Fig. 1. Distribution of *Austrelaps.*

dark smoky grey, little differentiated from dorsal colour. Chin shields and infralabials cream mottled with medium grey. Rostral, nasals, prefrontals, preocular, lower anterior temporal and supralabial dark brown with a white anterior margin. Most supralabials have the pale colour extending posteroventrally, forming pale triangles. Snout–vent length 450 mm. Tail 104 mm.

Austrelaps ramsayi (Krefft, 1864)

Hoplocephalus ramsayi Krefft 1864: 180.
Hoplocephalus bransbyi Macleay 1878: 52.
Denisonia superba.—Boulenger 1896: 353 (in part).
Austrelaps superbus.—Cogger et al. 1983: 218 (in part).
Austrelaps ramsayi.—Sutherland 1983: 50–52.

Remarks. Searches by the author and others for the holotype of *H. ramsayi*, a small, "apparently young" specimen from the "neighbourhood of Braidwood", New South Wales (Krefft 1864) have been unsuccessful and the specimen is presumed to be lost. Krefft's description is of a snake that in scalation and colour, especially the combination of a dark vertebral line, 15 midbody scale rows and "upper labials and chinshields whitish, marked with olive-brown in the upper corners", could only be a juvenile copperhead. The only respect in which the description fails to apply to a copperhead is the divided ("bifid") anal scale; this is considered to be either an aberration or an erroneous observation. Only one copperhead taxon, the highlands form, occurs in the Braidwood area and thus, in the absence of an earlier available name, the combination *Austrelaps ramsayi* (Krefft, 1864) is the correct name for this taxon.

The holotype of *Hoplocephalus bransbyi* Macleay, 1878 (AM R31922; ex Macleay Museum MR1362, R541), from Moss Vale, New South Wales (34° 33′ S, 150° 23′ E), has been examined and is also a typical highlands form specimen. In order to stabilise the name for the highlands form, the holotype of *H. bransbyi* is here designated as neotype of *H. ramsayi*. Thus, *H. bransbyi* becomes a junior objective synonym of *H. ramsayi*.

The neotype has the following taxonomically significant features: Midbody scale rows 15. Ventrals 151. Anal entire. Subcaudals 46, single. Lower anterior temporal inserted between fifth and sixth supralabials; not in contact with lower of two postoculars. Supralabials 6/6. Colour faded. Light brown dorsally. Narrow dark band

on neck, bordered posteriorly by a light band. Some dark "lines" along neck. Ventral surfaces light brown; anterior half of each ventral and subcaudal scale dark brown. Supralabials and lower anterior temporal dark brown with a sharply demarcated, triangular whitish anteroventral corner. Snout–vent length 340 mm. Tail 72 mm.

Notechis Boulenger, 1896

Type species. Naja (Hamadryas) scutata Peters, 1861.

Remarks. Notechis is closely related to *Austrelaps* and these genera were synonymised by Storr (1982). For several reasons, Storr's expanded concept of *Notechis* is unsatisfactory (Hutchinson 1990) and traditional usage, with *Notechis* restricted to the *scutatus–ater* complex and *Austrelaps* recognised as a distinct genus, is maintained here.

Schwaner (1985a, 1985b), based on work in preparation, believes that all tiger snake populations belong to the single species *Notechis scutatus*. Pending Schwaner's analysis, and to facilitate discussion, the view adopted here is that two species can be recognised, *N. scutatus* and the black tiger snake, *Notechis ater* (Krefft, 1866). *N. ater* is darker in colour than *N. scutatus* and has scale counts ranging lower. Further comparative work including biochemical analysis over the whole geographic range of *Notechis* is necessary to establish whether sufficient genetic divergence has occurred in the various disjunct populations to warrant the recognition of any of the subspecies listed in this paper. Also, the specific ranking of *N. ater* must be checked as Mitchell (pers. comm.) and Schwaner (pers. comm.) both report intermediacy of tiger snakes from the mouth of the Murray River and from Kangaroo Island, suggesting either local hybridisation or clinal intergradation.

Notechis is restricted to temperate Australia, the distribution shown in Fig. 2 being based on locality data from specimens in the Museum of Victoria and on selected references. In the author's view, the present disjunct populations of *Notechis* originated from two parent populations. Since the last glacial period, the rise in sea level and the southern climatic shift has fragmented the southern and western population (*N. ater*) and allowed the northeastern population (*N. scutatus*) to migrate southwards and expand into southeastern Australia. Distributions for *N. scutatus* provided by Worrell (1963c) and Cogger (1986: 446) showed the species extending
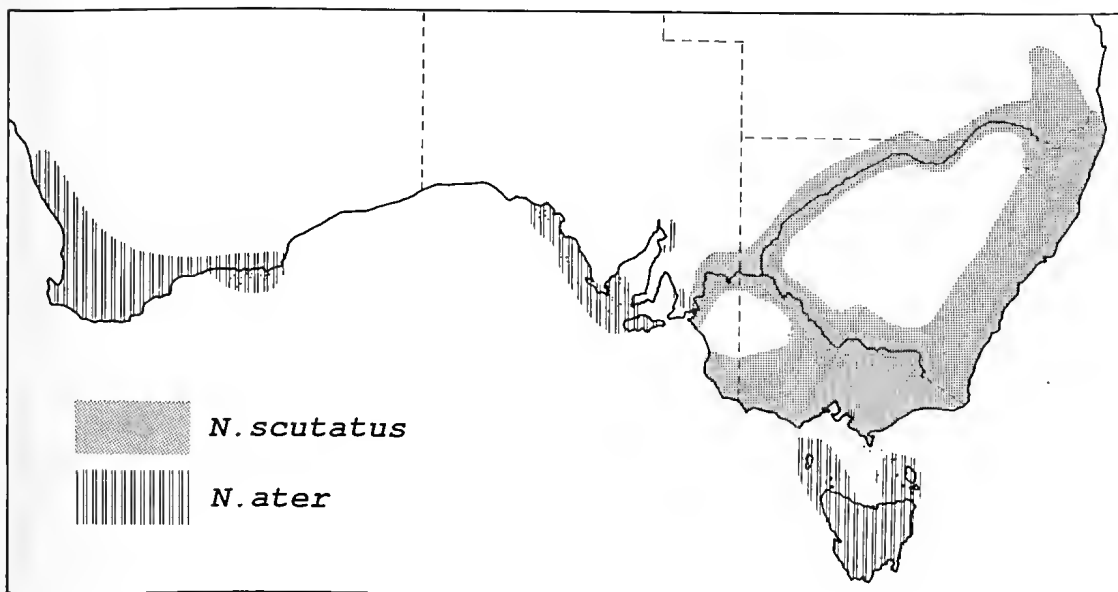
Fig. 2. Distribution of *Notechis.*

farther into the drier interior areas of New South Wales but excluded most of the Darling River and its tributaries.

Notechis scutatus (Peters, 1861)

Alecto curta.—Duméril et al. 1854: 1252–1254 (in part; non *Naja curta* Schlegel, 1837).
Hoplocephalus curtus.—Günther 1858: 216 (in part).
Naja (Hamadryas) scutata Peters 1861: 690.
Notechis scutatus.—Boulenger 1896: 351 (in part).—Rawlinson 1969: 122.
Notechis scutatus [scutatus].—Kinghorn 1956: 141–142.

Specimens examined. 67.

Scalation. Scales around midbody 17 (11), 19 (55), 21 (1). Ventral scales 158–185. Anal scale entire. Subeaudal scales 36–61, all single. The head and chin shields are similar to those of *N. ater* and there appear to be no consistent differences. As in *N. ater*, the head shields are subject to intraspeeific variation. Figures ean be found in Waite (1929) and Rawlinson (1965).

Colour. Very variable, green, grey-green or brown dorsal seales traversed by roughly 30 mm wide lighter or darker crossbands. There is also a morph with light brown dorsal scales and no crossbands (Rawlinson 1965, Worrell 1963d). Ventral scales lighter green, grey or brown, sometimes yellow. Subcaudals the same as the ventrals.

Remarks. Peters (1861) deseribed *Naja (Hamadryas) scutata* from a single specimen supposedly colleeted in Java. The holotype, ZMB 2815, cannot be located despite extensive searehes by the author and others, and the specimen is presumed lost (Cogger et al. 1983: 229). Peters' deseription (see Appendix 2) does not apply to any Javanese or even Asian elapid (van Hoesel 1959, Tweedie 1983, Welch 1988), whieh do not have the lower anterior temporal penetrating deeply between the last two supralabials, and most of whieh have seven supralabials (six in *Calliophis melanurus*) and at least some subeaudals divided. *Bungarus* Daudin, 1803, the only Asian genus generally lacking divided subeaudals, has only a single anterior temporal (Smith 1943). *Calliophis* Gray, 1835 and *Maticora* Gray, 1835 are also ruled out by their midbody scale count of 15 or fewer. The type locality of Java is therefore in error.

Among the proteroglyphous snakes, Peters' description uniquely fits the Australian elapids in the deeply wedged lower anterior temporal (charactcristic of the Australian elapids aceording to MeDowell 1970) combined with entire anal and subeaudal scales. Only the tiger snakes eombine these two features, plus 17 midbody scale rows and a transversely banded colour pat-

tern. The tiger snake maxilla has three to six tooth loci following the fang, agreeing with Peters' description of four teeth; the gap separating the last tooth can be interpreted as an empty alveolus rather than a true absence.

As Peters' description of the colour fits the tiger snakes of southern Queensland, New South Wales, Victoria and southeastern South Australia, it seems reasonable, and in view of the species' medical importance, highly desirable, to continue to apply the name *N. scutatus* to the tiger snakes of this area. Accordingly, specimen NMV D47618, a male, is hereby designated as neotype. The specimen was collected at "The Brothers", 10 km NE of Benambra, Victoria (36° 56′ S, 147° 45′ E) by P. A. Rawlinson, A. J. Coventry and P. B. Mather on 27 January 1976.

The neotype has the following taxonomically important characteristics. Midbody scale rows 19. Ventrals 172. Anal single. Subcaudals 57, entire. Frontal almost as wide as broad. Head uniform olive brown above. Neck and forebody olive brown with indistinct darker brown cross bands, more noticeable laterally than dorsally. Dark bands about 3 scales wide, the lighter interspaces about 2 scales wide. Posterior to this, the dark colour becomes predominant, and the lighter colour is confined to the edges of the scales of the interspaces of the banded pattern. Lower labials, throat and belly bright yellow, darkening to olive yellow posteriorly and to pale olive subcaudally. Snout–vent length 846 mm, tail 172 mm.

Notechis ater (Krefft, 1866)

Hoplocephalus ater Krefft 1866: 373.
Hoplocephalus fuscus Steindachner 1867: 82.
Alecto fasciolata Jan & Sordelli 1873: liv. 43, pl. 6, fig. 4.
Notechis scutatus.—Boulenger 1896: 351 (in part).
Notechis ater.—Kinghorn 1921: 143.—Rawlinson 1967: 215.—Cogger et al. 1983: 229.
Notechis scutatus niger Kinghorn 1921: 145.
Notechis scutatus ater.—Kellaway & Thomson 1932: 35–48.
Notechis scutatus occidentalis Glauert 1948: 139.—Storr 1982: 235.
Notechis ater ater.—Worrell 1963b: 130.
Notechis ater serventyi Worrell 1963c: 3.
Notechis ater humphreysi Worrell 1963c: 5.

Specimens examined. 74.

Scalation. Scales around midbody 15 (5), 17 (58), 19 (10), 21 (1). Ventral scales 135–184. Anal scale entire. Subcaudal scales 31–59, all single. The head shield is very similar to that of *N. scutatus* but intraspecific variation seems

greater in this species. Supralabials 6 (5). Figures can be found in Kinghorn (1921, 1929, 1956) Kellaway & Thomson (1932), Tubb (1938), Glauert (1957) Worrell (1963c) and Cogger (1986).

Colour. Variable, jet black, slate grey or dark brown dorsal scales, usually with lighter crossbands which are more visible on the anterior half of the body. The bands are narrower than in *N. scutatus* (20 mm or less). Sharland (1962) reported that some Tasmanian specimens are ash grey or light sandy in colour with no trace of bands. The ventral scales are lighter than the dorsal scales. Sharland (1962) and Glauert (1948) recorded that some Tasmanian and Western Australian specimens have yellow anterior ventral scales and crossbands. Schwaner (1984) has commented on reddish-bellied black tiger snakes from Kangaroo Island which had been confused with *Pseudechis porphyriacus* (Shaw, 1794). Subcaudals are usually darker than the ventrals.

Remarks. Hoplocephalus ater, described by Krefft (1866) on the basis of a single specimen (AM 6577) from the Flinders Ranges, South Australia, was placed in synonymy with *Notechis scutatus* by Boulenger (1896). Kinghorn (1921) reinstated Krefft's species, placing it in *Notechis* and redescribing the type specimen as the original description was inaccurate. Kinghorn also described a single specimen from Kangaroo Island, South Australia as a new subspecies, *Notechis scutatus niger*, which resembled *N. ater* but was distinguished by the presence of six instead of five supralabials. Kinghorn noted that in coloration and form, the new subspecies most closely resembled Tasmanian tiger snakes. Kellaway & Thomson (1932) identified a series of 49 snakes from Chappell Island in the Furneaux Group, Bass Strait as *N. scutatus niger*, describing and illustrating the variations in head and chin shields and supralabials, and stating that the variation overlapped Kinghorn's descriptions of *N. scutatus niger* and *N. ater*. They therefore reduced *N. ater* to subspecific ranking as *N. scutatus ater*.

Worrell (1963b) reported the discovery of three new specimens of *N. ater* in the Flinders Ranges, stating that, as all had six supralabials, the type was aberrant. He referred to this taxon as *N. ater ater* and listed Kinghorn's *N. scutatus niger* as a subspecies of *ater*. As Kinghorn's separation of *niger* from *ater* on the number of supralabials is invalid, and as Kellaway &

Thomson (1932) showed that variations in a single population overlapped the descriptions of *ater* and *niger*, there seems to be no reason for retaining *niger* as a subspecies and it is here synonymised with *ater*.

Worrell (1963e) described two new subspecies, *N. ater serventyi* from Chappell Island and *N. ater humphreysi* from New Year Island, both in Bass Strait. As these subspecies were based on venom and ecological differences, and as the comparative aspects of the work were not sufficiently comprehensive, there appears to be no reason for the retention of these names.

Glauert (1948) named the southwestern tiger snakes *N. scutatus occidentalis*, basing his description on 40 specimens in the Western Australian Museum, Perth. He compared these with Kinghorn's (1929) scale counts for *N. scutatus scutatus*, assuming these figures to be typical for southeastern Australian specimens. More recent work (Mitchell 1951, Rawlinson 1965), however, has demonstrated that Kinghorn's scale counts were inaccurate, probably being based on Boulenger's (1896) figures for *Brachyaspis curta*. Kinghorn (1956), apparently realising his error, deleted these scale counts from the second edition of his book but provided no alternatives; he also mentioned *N. scutatus occidentalis*, apparently not recognising it. Thus, although Glauert provided a valuable list of scale counts for southern Western Australian tiger snakes, he did not have accurate data on eastern populations for comparison. As Glauert's colour description and scale counts overlap descriptions of eastern populations referred to *N. ater*, this name has been applied to the Western Australian populations by Rawlinson (1974), though Storr et al. (1986) continued to use the combination *N. scutatus occidentalis*.

Two other names, *Hoplocephalus fuscus* Steindachner, 1867 and *Alecto fasciolata* Jan & Sordelli, 1873, have been included by Cogger et al. (1983) in the synonymy of *Notechis scutatus*. Despite searches by the author and others in European collections used by Steindachner and Jan & Sordelli, the type specimens of neither species can be located (Cogger et al. 1983) and are therefore presumed lost.

Most of Steindachner's description of *H. fuscus* (Appendix 2), especially the "vertical" (= frontal) shield that is almost as wide as long and the banded pattern, clearly indicates a tiger snake. All three type specimens, however, were said to have only 15 midbody scale rows, a statistically most unlikely result for mainland tiger snakes. One or both of the larger (unbanded) specimens could have been copperheads, which have 15 midbody scale rows. However, 15 midbody scale rows are also found in a minority of Tasmanian tiger snakes which are frequently unbanded, and the ventral count given (ca 177) is higher than that recorded in any copperhead population but within the normal range for tiger snakes. It is therefore considered that *Hoplocephalus fuscus* Steindachner, 1867 is a junior subjective synonym of *Hoplocephalus ater*.

The name *Alecto fasciolata* first appeared as a *nomen nudum* in a list in Jan (1863), where the only identifying character noted was a midbody scale count of 17. The illustration in Jan & Sordelli (1873, liv. 43, pl. 6, fig. 4) shows a very well-banded tiger snake in which the pale cross-bands are markedly narrower than the very dark interspaces. Such a combination of colour pattern and scale count is more typical of *N. ater* than of *N. scutatus*. Therefore *Alecto fasciolata* is also regarded as a junior subjective synonym of *Hoplocephalus ater*.

In order to stabilise the status of *Hoplocephalus fuscus* and *Alecto fasciolata*, specimen SAM R14373, a male, from Diprose Lake, Tasmania (41°49′ S, 147°22′ E), collected by H. Ehmann in February 1973, is here designated neotype of both species. The neotype has the following taxonomically important characteristics. Midbody scale rows 17. Ventrals 173. Anal single. Subcaudals 53, entire (hemipenis reaches to fourteenth subcaudal). Frontal truncate anteriorly, about as wide as long. Head uniform dark brown above. Neck and forebody similar to head in base colour but with indistinct, narrow (about half a scale wide), pale cross-bands becoming more pronounced and broader (to one and a half scales wide) laterally. Dark interspaces about two to three scales wide. Banding disappears dorsally about mid-body and last traces of lateral bands disappear by the last third of the body. Lower labials, throat, and chin olive grey. Anterior ventrals dull yellow with irregular black edgings posteriorly and laterally. Ventral colour darkening to olive grey with less distinct dark edges by mid body, and to dark grey on the posterior belly and subcaudals. Snout–vent length 962 mm, tail 177 mm.

ACKNOWLEDGMENTS

and Dr M. N. Hutchinson (South Australian Museum, Adelaide), and Mr B. C. Mollison (Inland Fisheries Commission, Hobart) for the loan of specimens and for discussions resulting in this paper. Staff of the European museums visited in 1973–4 are also thanked for their hospitality and assistance. The receipt of a Commonwealth Postgraduate Research Award during the early stages of data gathering is gratefully acknowledged. This paper was compiled by A. J. Coventry and M. N. Hutchinson from Peter Rawlinson's unpublished notes and manuscripts; Marnie and Kate Rawlinson assisted in assembling the material.

REFERENCES

BOULENGER, G. A., 1896. *Catalogue of the Snakes in the British Museum (Natural History)*, vol. 3. British Museum, London, xiv + 727 p.

COGGER, H. G., 1986. *Reptiles and Amphibians of Australia*, 4th edn. Reed Books, Frenchs Forest, New South Wales, 688 p.

COGGER, H. G., CAMERON, E. E. & COGGER, H. M., 1983. *Zoological Catalogue of Australia*, vol. 1, *Amphibia and Reptilia*. Australian Government Publishing Service, Canberra, vi + 313 p.

COVENTRY, A. J. & RAWLINSON, P. A., 1980. Taxonomic revision of the elapid snake genus *Drysdalia* Worrell, 1961. *Memoirs of the National Museum of Victoria* 41: 65–78.

DAUDIN, A., 1803. Caracteres des vingt-trois genres qui composent l'ordre des Ophidiens. *Magazin Encyclopédique* (An. 8) 5: 433–438.

DUMÉRIL, A. M. C. & BIBRON, G. & DUMÉRIL, A. 1854. *Erpétolgie générale ou histoire naturelle complète des Reptiles*, vol. 7, part 2. Roret, Paris, xii + 781–1536.

GLAUERT, L., 1948. The western tiger snake, *Notechis scutatus occidentalis* subsp. nov. *Western Australian Naturalist* 1: 139–141.

GLAUERT, L., 1957. *A Handbook of the Snakes of Western Australia*, 2nd edn. Western Australian Naturalists' Club, Perth.

GRAY, J. E., 1835. *Illustrations of Indian Zoology; Chiefly Selected from the Collection of Major-General Hardwicke*, vol. 2. London, 95 pls.

GÜNTHER, A. 1858, *Catalogue of Colubrine Snakes in the Collection of the British Museum*. British Museum, London, xvi + 281 p.

GÜNTHER, A., 1863. Third account of new species of snakes in the British Museum. *Annals and Magazine of Natural History (3)* 12: 348–365.

HUTCHINSON, M. N., 1990. The generic classification of the Australian terrestrial elapid snakes. *Memoirs of the Queensland Museum* 29: 397–405.

JAN, G., 1859a. Plan d'une iconographie descriptive des ophidiens, et description sommaire de nouvelles espèces de serpents. *Revue et Magasin de Zoologie Pure et Appliquée (2)* 11: 122–130.

JAN, G., 1859b. *Prodrome d'une Iconographie descriptive des Ophidiens et description sommaire de nouvelles espèces de serpents venimeux*. Bouchard-Huzard, Paris, 32 p.

JAN, G., 1863. *Elenco sistematico degli Ofidi descritti e designati per l'Iconografia generale*. A. Lombardi, Milan, vii + 143 p.

JAN, G. & SORDELLI, F., 1873. *Iconographie générale des Ophidiens*, vol. 3, livraisons 43 & 44. F. Sordelli, Milan.

KELLAWAY, C. H. & THOMSON, D. F., 1932. Observations on the venom of a melanistic insular variety of the tiger snake, *Notechis scutatus*. *Australian Journal of Experimental Biology and Medical Science* 10: 35–48.

KINGHORN, J. R., 1921. Studies in Australian reptiles. 2. *Records of the Australian Museum* 13: 143–154.

KINGHORN, J. R., 1929. *The Snakes of Australia*. Angus & Robertson, Sydney, 198 p.

KINGHORN, J. R., 1956. *The Snakes of Australia*, 2nd edn. Angus & Robertson, Sydney, 197 p.

KREFFT, G., 1864. Descriptions of three new species of Australian snakes. *Proceedings of the Zoological Society of London* (1864): 180–182.

KREFFT, G., 1866. Descriptions of three species of snakes of the genus *Hoplocephalus*. *Proceedings of the Zoological Society of London* (1866): 370–371.

MCDOWELL, S. B., 1970. On the status and relationships of the Solomon Island elapid snakes. *Journal of Zoology; Proceedings of the Zoological Society of London* 161: 145–190.

MITCHELL, F. J., 1951. The South Australian reptile fauna. Part 1, Ophidia. *Records of the South Australian Museum* 2: 554–556.

PETERS, W., 1861. Zweite Übersichte der von Herrn F. Jagor auf Malacca, Java, Borneo und den Philippinen gesammelten und dem Kgl. zoologischen Museum übersandten Schlangen. *Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin* (1861): 683–691.

RAWLINSON, P. A., 1965. Snakes of the Melbourne area. *Victorian Naturalist* 81: 245–253.

RAWLINSON, P. A., 1967. The vertebrate fauna of the Bass Strait islands. 2. The Reptilia of Flinders and King Islands. *Proceedings of the Royal Society of Victoria* 80: 211–224.

RAWLINSON, P. A., 1969. The reptiles of East Gippsland. *Proceedings of the Royal Society of Victoria* 82: 113–128.

RAWLINSON, P. A., 1971. The reptiles of West Gippsland. *Proceedings of the Royal Society of Victoria* 84: 37–52.

RAWLINSON, P. A., 1974. Biogeography and ecology of reptiles of Tasmania and the Bass Strait area. In *Biogeography and Ecology in Tasmania*, W. D. Williams, ed., W. Junk, The Hague, 291–338.

SCHLEGEL, H., 1837. *Essai sur la physionomie des*

Serpens. Partie Générale et Partie Descriptive. Kips & Stockum, La Haye, xxviii + 251 + 606 p.

SCHWANER, T. D., 1984. Identity of red-bellied black snakes on Kangaroo Island. *Transactions of the Royal Society of South Australia* 108: 137.

SCHWANER, T. D., 1985a. *Snakes in South Australia: A Species List and Overview.* South Australian Museum, Adelaide, 8 p.

SCHWANER, T. D., 1985b. Population structure of black tiger snakes, *Notechis ater niger*, on off-shore islands of South Australia. In *Biology of Australasian Frogs and Reptiles*, G. C. Grigg, R. Shine & H. Ehmann, eds, Royal Zoological Society of New South Wales, Sydney, 35–46.

SHARLAND, M., 1962. *Tasmanian Wildlife.* Melbourne University Press, Melbourne.

SHAW, G., 1794. *The Zoology of New Holland.* London, 33 p.

SHINE, R., 1987a. Ecological ramifications of prey size: food habits and reproductive biology of Australian copperhead snakes. *Journal of Herpetology* 21: 21–28.

SHINE, R., 1987b. Ecological comparisons of island and mainland populations of Australian tigers-nakes (*Notechis*: Elapidae). *Herpetologica* 43: 233–240.

SMITH, M. A., 1943. *Fauna of British India*, vol. 3, *Serpentes.* Taylor & Francis, London, xii + 583 p.

STEINDACHNER, F., 1867. Reptilien. In *Reise der Österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859*, Zoologische Theil, Band 1, *Wirbelthiere*, vol. 3, B. von Wüllerstorf-Urbair, ed., Royal Imperial Court and State Printery, Vienna, 1–98.

STORR, G. M., 1982. The genus *Notechis* (Serpentes: Elapidae) in Western Australia. *Records of the Western Australian Museum* 9: 325–340.

STORR, G. M., SMITH, L. A. & JOHNSTONE, R. E., 1986. *Snakes of Western Australia.* Western Australian Museum, Perth, ix + 187 p.

SUTHERLAND, S., 1983. *Australian Animal Toxins.* Oxford University Press, Melbourne, xx + 527 p.

TUBB, J. A., 1938. Report of the McCoy Society, Sir Joseph Banks Islands. *Proceedings of the Royal Society of Victoria* 50: 383–385.

TWEEDIE, M. W. F., 1983. *The Snakes of Malaya*, 3rd edn. Singapore National Printers, Singapore, 167 p.

VAN HOESEL, J. K. P., 1959. *Ophidia Javanica.* Museum Zoologicum Bogoriense, Bogor, 188 p.

WAITE, E. R., 1929. *The Reptiles and Amphibians of South Australia.* Government Printer, Adelaide, 270 p.

WELCH, K. R. G., 1988. *Snakes of the Orient, A Checklist.* Robert E. Krieger Publishing, Malabar, Florida, vii + 183 p.

WORRELL, E. R., 1963a. A new elapine generic name. *Australian Reptile Park Records* 1: 1–7.

WORRELL, E. R., 1963b. *Reptiles of Australia.* Angus & Robertson, Sydney, xv + 169 p.

WORRELL, E. R., 1963c. Two new subspecies of the elapine genus *Notechis* from Bass Strait. *Australian Reptile Park Records* 2: 2–11.

WORRELL, E. R., 1963d. *Dangerous Snakes of Australia and New Guinea*, 5th edn. Angus & Robertson, Sydney, 66 p.

APPENDIX 1

Notes on the syntypes of *Hoplocephalus superbus.*

BMNH 1946.1.20.37. (Boulenger's specimen e; lectotype herein). Label on jar stating "1946.1.20.37–38, *Denisonia superba* (Types) Tasmania R. Gunn". Snout–vent length (SVL) 594 mm; tail length (T) 131 mm; midbody scale rows (MSR) 15; ventrals (V) 143; subcaudals (SC) 46, all single; anal scale (A) 1; upper labials (UL) 6 (3 and 4 suborbital); lower labials (LL) 7. Frontal 7 mm long by 3.8 mm wide. Rostral 4.5 mm wide by 4.0 mm high, in contact with first upper labial, nasal and internasal scales. Preocular single, in contact with third and fourth upper labials, nasal, prefrontal and supraocular scales. Postoculars 2, in contact with supraocular, parietal, upper anterior temporal, and fourth and fifth upper labials. Temporals 2 + 2. Upper lip colouration typical of *A. superbus* (s.s.), without [contrasting] dark patches. Specimen in reasonable condition, with some soft patches and peeling epidermis.

The remaining specimens conform to this description except where noted.

BMNH 1946.1.20.40. (Boulenger's specimen a). Label on jar stating "*Denisonia superba* (Type) Australasia 'Erebus & Terror' Expedition". SVL 848 mm; T 159 mm; MSR 15; V 153; SC 48, all single; A 1; UL 6 (3 and 4 suborbital); LL 7. [Nasal–preocular contact?]. Postoculars 2, in contact with upper[?] anterior temporal. Temporals 2 + 2. Upper lip colouration typical of *A. superbus* (s.s.). Specimen in poor condition, being soft and with scales peeling. (*Note by AJC and MNH*, The author's notes on the type series are very specific in all cases excepting this specimen where they state "Postoculars = 2; supraocular; parietal; temporal; 4 + 5 labial". We interpret this to mean that the lower postocular contacts only the upper anterior temporal. The presence or absence of a nasal–preocular contact is not explicitly stated.)

BMNH 1946.1.20.42. (Boulenger's specimen b). Label on jar stating "*Denisonia superba* (Type) Australasia 'Erebus & Terror' Expedition". SVL 582 mm; T 123 mm; MSR 15; V 150; SC 45, all single, A 1; UL 6 (3 and 4 suborbital); LL 7. Postoculars 2, in contact with both anterior temporals. Temporals 2 + 2. Upper lip colouration typical of *A. superbus* (s.s.). Specimen in poor condition, being soft and with head damage.

BMNH 1946.1.19.6. (Boulenger's specimen c). Label on jar stating "*Denisonia superba* (Type) Australasia

'Erebus & Terror' Expedition". SVL 677 mm; T 133 mm; MSR 15; V 148; SC 45 all single; A 1; UL 6 (3 and 4 suborbital); LL 6. Postoculars 2, in contact with both anterior temporals. Temporals 2 + 2. Upper lip colouration typical of *A. superbus* (s.s.). Specimen in poor condition, epidermis peeling, and with head damage.

BMNH 1946.1.19.5. (Boulenger's specimen d). Label on jar stating "*Denisonia superba* (Type) Tasmania A. J. Smith". SVL 552 mm; T 108; MSR 15; V 148; SC 41 all single; A 1; UL 6 (3 and 4 suborbital); LL 7. Postoculars 2, in contact with both anterior temporals. Temporals 2 + 2. Upper lip colouration typical of *A. superbus* (s.s.). Specimen in poor condition, epidermis peeling badly.

BMNH 1946.1.20.38. (Boulenger's specimen f). Label on jar stating "1946.1.20.37–38, *Denisonia superba* (Types) Tasmania R. Gunn". SVL 425 mm; T 99 mm; MSR 15; V 150; SC 46 all single; A 1; UL 6 (3 and 4 suborbital); LL 6. Postoculars 2, in contact with both anterior temporals. Temporals 2 + 2. Upper lip colouration typical of *A. superbus* (s.s.).

BMNH 1946.1.20.34. (Boulenger's specimen h). Label on jar stating "1946.1.20.34–36. *Denisonia superba* (Types) Australia". SVL 644 mm; T 140 mm; MSR 15; V 151; SC 49 all single; A 1; UL 6 (3 and 4 suborbital); LL 6. Postoculars 2, in contact with upper anterior temporal. Temporals 2 + 2. Upper lip colouration typical of *A. superbus* (s.s.). Specimen in reasonable condition, with some soft patches and peeling epidermis.

BMNH 1946.1.20.35. (Boulenger's specimen g). Label on jar stating "1946.1.20.34–36. *Denisonia superba* (Types) Australia". SVL 672 mm; T 140 mm; MSR 15; V 149; SC 47 all single; A 1; UL 6 (3 & 4 suborbital); LL 7. Postoculars 2, in contact with upper anterior temporal and with fourth and fifth upper labials. Temporals 2 + 3. Upper lip colouration typical of *A. superbus* (s.s.). Specimen in reasonable condition, with some soft patches and peeling epidermis.

BMNH 1946.1.20.36. (Boulenger's specimen i). Label on jar stating "1946.1.20.34–36, *Denisonia superba* (Types) Australia". SVL 154 mm; T 29 mm; MSR 15; V 150; SC 43 all single; A 1; UL 6 (3 and 4 suborbital); LL 7. Postoculars 2, in contact with both anterior temporals. Temporals 2 + 2. Upper lip colouration with dark patches typical of juvenile *A. superbus* (s.s). Specimen in good condition, with some soft patches.

APPENDIX 2

Original descriptions of species for which original type specimens no longer exist.

Alecto labialis, from Jan 1859b: 21.

"This snake, with a steel-coloured body, is distinguished from its congeners by the labials, half yellow, half black; the lower part of the head [sic, read 'body'] is very dark coloured, except for the head which is also variegated with yellow and black; tip of tail white; 15 scale rows; after the cloaca, 11. Ventrals, 136; anal single; [sub-]caudals entire, 42; total length, 55"; tail 9"." [Translated from French.]

Naja (Hamadryas) scutata, from Peters 1961: 690.

"One anterior preorbital shield much higher than long, 2 postorbitals. Only 6 supralabial shields, the 3rd and 4th abutting the eye; the first lower temporal shield is the same size as a supralabial and extends ventrally between the last two. Scale rows just behind the head 16, at the middle of the body 17. All subcaudals entire. Above olive-coloured, with light, distinct transverse bands on the second half of the body. Underside light greenish yellow, the belly and subcaudal scales with blackish bases. Ventral shields 173, the last (anal) entire, subcaudals 45. Behind the fang the upper jaw bears four solid, grooved teeth, which increase in size from first to last and on each side the first three follow closely after one another, [while] the last (fourth) is separated from them by a larger gap. – Total length 1.30 m; head 0.046 m; tail 0.168 m. – Java." [Translated from German.]

Hoplocephalus ramsayi, from Krefft 1864: 180.

"Scales in 15 rows. Anal bifid. Ventrals 164. Subcaudals 51. Total length 10½'; tail 2'. Body rather elongate and rounded; head scarcely distinct from neck, rather high and elongate, with obtuse muzzle; rostral just reaching to the surface of crown; anterior frontals moderate, rounded in front; posterior ones larger, bent down on the sides; one anterior, two posterior oculars, the lower forming about one-fourth of the orbit; vertical narrow, six-sided, much longer than broad; superciliaries nearly the same size as the vertical; occipitals moderate, not forked behind; six upper labials, the third and fourth forming the lower part of the orbit; no loreal, replaced by the elongate nasal, second and third upper labial, anterior ocular and bent down anterior frontal. One nasal, pierced by the nostril; scales moderate, rhomboid, in fifteen rows; tail rather short, scarcely distinct from trunk, tapering; eye moderate, pupil rounded; grooved fang in front, some smaller smooth teeth behind.

Dark olive-green above, each scale tipped with reddish, in particular those on the sides; crown and a narrow vertebral line, one scale wide, somewhat darker than the other parts; this line extends to the root of the tail; upper labials and chin shields whitish, marked with olive-brown in the upper corners. Beneath yellow, each ventral scale with a blackish margin; subcaudals nearly black.

Mr E. P. Ramsay discovered this new Snake in the neighbourhood of Braidwood, N. S. Wales; it is apparently a young specimen, its total length not exceeding 10½ inches."

Hoplocephalus fuscus, from Steindachner 1867: 82.

"Syn. *Hoplocephalus Cuvieri* Fitz. (excl. Syn. et Hopl. Cuvieri Fitz. Syst. Rept. p. 28), Ausb. p. 410.

The specimen from the old collection of the Vienna Museum referred to by Fitzinger in "Systema Reptilium" (1843, p. 28) as *Hoplocephalus Cuvieri* belongs to the *Hopl. curtus* species [of] Schlegel and has nineteen scale rows, while the three specimens bearing only fifteen longitudinal scale rows referred to by the same name by Fitzinger in *Cataloge der österr. Naturf.* (p. 410) perhaps belong to an as yet undescribed species, which, in my opinion, is very closely related to *Hopl. pallidiceps* Günth., if not identical.

Char. The head is elongate and tapers anteriorly, in cross-section it has a quadrangular appearance, the dorsal surface is quite flat, and the mid region of the head not widely bulging; the body is rounded, of thick-set appearance, the tail short with a pronounced taper to a point. The vertical shield is only slightly longer than broad. Of the six supralabials the third and fourth are situated below the eye; the second and third are developed dorsally rather as in *H. pallidiceps*, at times (that is to say among the three specimens on one or both sides of the head) acting as a substitute for the absent loreal shield; in the latter case the undivided nasal shield is abruptly truncated posteriorly, in the former it extends to a narrow point. Temporal shields 2 + 2. The upper temporal of the first series is elongate [and] quadrangular, and contacts both postocular shields anteriorly; the lower, larger temporal shield of the same series is triangular with a dorsally curved broad base and rests with the tapering point of its anterior angle against the lower postocular. The upper temporal shield of the second series sometimes fuses with the scales margining it posteriorly, forming a single very large shield. The body scales diminish rapidly in size moving away from the edge of the belly. The dorsal surface of the head and back is dark brown, towards the edge of the belly the sides of the body are olive green. In the neck region of the smallest specimen of 26 inches [Zoll Länge] the outermost scale row bears a yellow-brown longitudinal band; ventral to this is a wider blackish band, which includes the lateral edge of the anterior ventral shields. In just this one specimen one observes on the back distinct traces of small light yellowish brown crossbands which become markedly broader towards the edge of the belly. The largest specimens of 36–38 inches however are quite uniformly coloured dorsally. The anterior and posterior edges of the ventral scales, or only their anterior edges, have blackish seams. – Subcaudal shields (entire) 48–51; ventral scales circa 177. Origin: New Holland." [Translated from German.]

AVAILABLE FOR PURCHASE

Many volumes of the Proceedings of the Royal Society of Victoria are still available. Each volume includes various original papers of outstanding or historical interest. This fundamental reference material offers new perspectives and the results of research in: *GEOLOGY; GEOMORPHOLOGY; PALAEONTOLOGY; BOTANY; ZOOLOGY; ECOLOGY;* and *ANTHROPOLOGY.*

Of these papers, the following are typical:

The Search for an Evolutionary Philosophy of Man. By R. D. Alexander. *In* Vol. 84, 1971.

Tertiary and Late Cretaceous Spores and Pollen from the Gippsland Basin, Southeastern Australia. By L. E. Stover & A. D. Partridge. *In* Vol. 85, 1973.

Design and the Living Environment. By D. G. D. Yencken. *In* Vol. 86, 1974.

Density and Diversity of Bird Populations in *Eucalyptus* Forests in Victoria, Bass Strait Islands and Tasmania. By Ian Abbott. *In* Vol. 87, 1975.

Victorian Coastal Geomorphology. By Eric C. F. Bird. *In* Vol. 92, 1981.

Mammals of Southwestern Victoria from the Little Desert to the Coast. By P. W. Menkhorst & C. M. Beardsell. *In* Vol. 94, 1982.

Palaeozoic Acid Volcanism in Victoria. By W. D. Birch, *In* Vol. 95, 1983.

New Placoderm Fishes from the Early Devonian Buchan Group, Eastern Victoria. By John Long. *In* Vol. 96, 1984.

The Genus *Eudendrium* (Hydrozoa: Hydroida) from Australia. By Jeanette Watson. *In* Vol. 97, 1985.

Vertebrate Fauna of the Silverband Formation, Grampians, Western Victoria. By Susan Turner. *In* Vol. 98, 1986.

AUTHOR INDEX, 1855–1986

This valuable bibliographic tool is available in the relevant volumes, or in reprints, as follows:

1855–1934	Publications of the Royal Society of Victoria together with those of the Societies amalgamated with it. Compiled by F. A. Cudmore. *In* Vol. 46, Pt 2, 1934.
1934/5–1958	Proceedings of the Royal Society of Victoria, Vol. 47–Vol. 70. Prepared by C. A. McCallum. *In* Vol. 73, 1960. *Price of reprint,* pp. 51–63, $2.50.
1959–1971	Proceedings of the Royal Society of Victoria, Vol. 71–Vol. 84. *In* Vol. 84, Pt 2, 1971. Prepared by R. R. Garran. *Price of reprint,* pp. 275–282, $2.50.
1972–1986	Proceedings of the Royal Society of Victoria, Vol. 85–Vol. 98. *In* Vol. 99, Pt 4, 1987. Prepared by G. F. Watson. *Price of reprint,* pp. 147–156, $2.50.

All volumes mentioned above, and many others, are available for purchase. For prices and ordering details, see inside front cover.

PROCEEDINGS

OF THE

ROYAL SOCIETY OF VICTORIA

Volume 104

1992

CONTENTS OF VOLUME 104

DISTRIBUTION OF FRESHWATER FISHES IN EAST GIPPSLAND, VICTORIA, 1967–1991

T. A. RAADIK

Freshwater Ecology Branch, Department of Conservation & Environment, 123 Brown Street, Heidelberg, Victoria 3084

Distribution maps of freshwater fish species in the three river basins within the East Gippsland region of Victoria were constructed from data recorded at 153 sites surveyed during 1967–1991. Species diversity was high, 19 species of native freshwater fish (83% of the native freshwater species found in all Victorian coastal river basins) having been recorded. The fauna was dominated by diadromous native species (12 species), the majority of these being widespread and abundant. *Anguilla australis, Galaxias maculatus, Retropinna semoni* and *Salmo trutta* were the most widespread fish species, and the last three were the most abundant. Of 14 species of native fish classified as threatened in Victoria, 10 were recorded from East Gippsland, representing 53% of the native species in the region. Most species considered threatened in Victoria had restricted distributions and low abundances in East Gippsland. Five introduced freshwater fish have been recorded from the region but four of them (*Carassius auratus, Cyprinus carpio, Oncorhynchus mykiss* and *Perca fluviatilis*) had restricted distributions. *Salmo trutta* was more widely distributed than the other introduced species but was restricted to the western half of the region. General comments on the distribution of each species are presented, and the need for an increase in coordinated survey effort in the region is recognised.

ACCURATE information about the distribution and abundance of the freshwater fish fauna of Victoria is crucial to the ecologically well-balanced management of the State's aquatic environment and biota, and is also essential in assessing the conservation status of freshwater fish species (Koehn & Morison 1990). Such information, particularly for species of smaller native fish, was sparse until the late 1970s when the results of surveys began to be published (e.g. Tunbridge 1978, Cadwallader 1979, Tunbridge 1983, McCarraher 1986a, b, c, d, Koehn 1986a, b, Brumley et al. 1987, Morison & Anderson 1987, Tunbridge 1988, Tunbridge & Glenane 1988, Hall & Tunbridge 1988, Anderson & Morison 1989, Hall 1989, McKenzie & O'Connor 1989, and Koehn & O'Connor 1990a).

In reviewing the available information on the aquatic fauna and habitat of East Gippsland, Blyth & Jackson (1985) found that much of the region's aquatic habitat had not been adequately surveyed. Nevertheless, the information, although scant, indicated a high species diversity in the native fish fauna. Indeed, Blyth & Jackson (1985) concluded that the region contained comparatively pristine ecosystems of considerable importance as a scientific reference area against which other aquatic habitats in

south-eastern Australia could be compared, a conclusion also reached by Macmillan (1990). Yet since 1985, published results of surveys of the region's freshwater fish fauna have been few (Baxter et al. 1989, Hall 1989, Baxter et al. 1991, Kochn et al. 1991), despite continuing exploitation of the region's natural resources; e.g. intensive harvesting of timber resources since the 1960s and especially in recent years (LCC 1985, Department of Conservation, Forests & Lands 1988). Macmillan (1990) noted the limited amount of fish survey work in East Gippsland, and Koehn & Morison (1990) stressed the need for further comprehensive fish surveys in the region.

The fish distribution information from East Gippsland reviewed by Blyth & Jackson (1985) is now incomplete, additional species and range extensions having been recorded since then. In contrast to the opinion of the Office of the Commissioner for the Environment (OCE 1989), the recent compilation of fish distribution data for East Gippsland (DWR 1989) was also found to be incomplete and in part inaccurate.

In this report I present detailed distribution maps and comments on the native and introduced fish species of East Gippsland. In compiling the distribution maps I have relied heavily on published and unpublished information

gathered by many investigators during 1967–1991. A resource document containing detailed historical and current species distribution information in estuarine and freshwater habitats in East Gippsland will be published as part of the Silvicultural Systems Project of the Victorian Department of Conservation and Environment (DCE).

STUDY AREA

In this paper, East Gippsland refers to that part of Victoria containing river basins 20 (Towamba River), 21 (East Gippsland), and 22 (Snowy River) (Fig. 1) as designated by the Australian Water Resources Council (1976). As such, the region is more extensive than that encompassed by the Land Conservation Council's review of East Gippsland (LCC 1985) but is smaller than the area designated as the East Gippsland Forest Management Area (Department of Conservation, Forests & Lands 1988), which includes some of river basin 23, the Tambo River. River basins 20, 21 and 22 are not

wholly contained within Victoria, 90%, 25% and 60% respectively of their catchments lying in New South Wales.

The location map of the study area (Fig. 1) shows only the main river systems in each of the three river basins, and consequently does not depict the actual density of watercourses in East Gippsland. Macmillan (1989) has presented a more detailed map of the region's seasonal and perennial streams.

DATA SOURCES AND LIMITATIONS

Detailed distribution information for native and introduced freshwater fish species in East Gippsland was compiled from the following sources: published books and refereed scientific journals (Spencer et al. 1889, Timms 1973, Bell et al. 1980, Tunbridge & Rogan 1981, Blyth & Jackson 1985); unpublished university theses (Chessman 1971, Malcolm 1971, Ramm 1986); technical and management reports (Tunbridge 1983, Baxter 1985, 1986, McCarraher 1986a, Jackson & Koehn 1988, Baxter et al. 1989, Hall
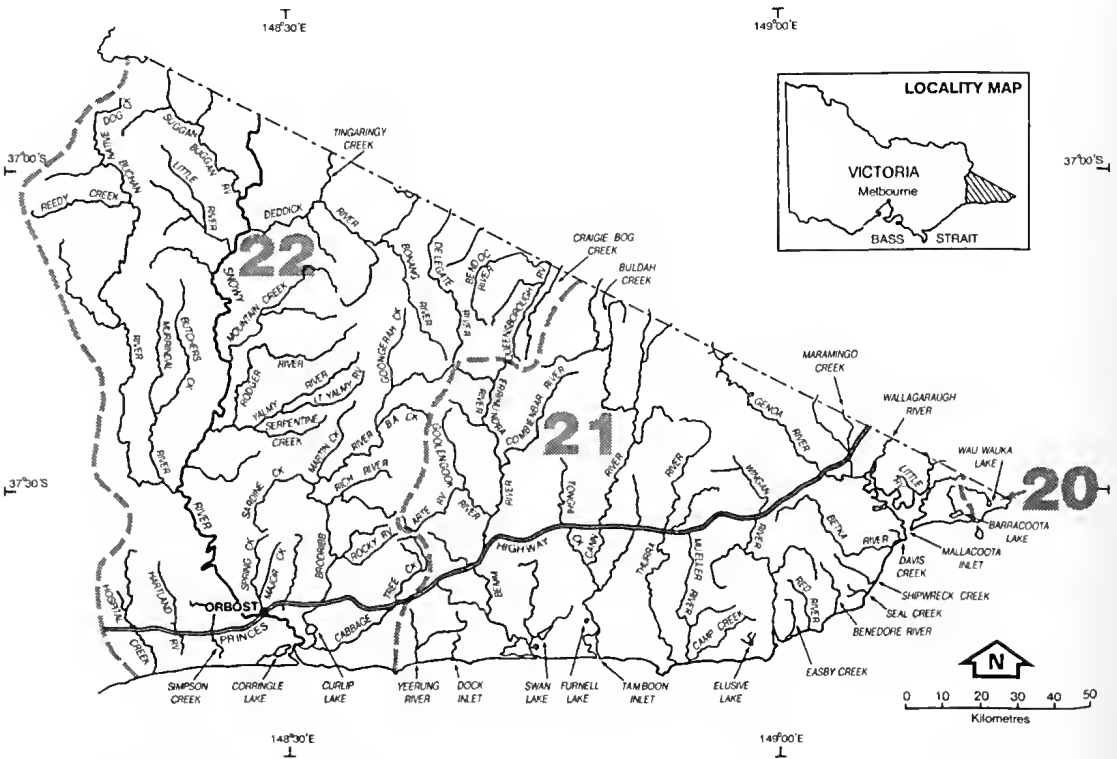

Fig. 1. Map of the East Gippsland region showing the major river systems in the Victorian portions of the Towamba (20), East Gippsland (21) and Snowy (22) river basins.

1989, Barnham 1990, Baxter et al. 1991, Koehn et al. 1991); and other publications (Anon 1974, Dixon 1976, Tunbridge & Glenane 1983). Unpublished information was also obtained from members of the Flora and Fauna and Fisheries Divisions, DCE, and from fish collection data from the Museum of Victoria, Melbourne and the Australian Museum, Sydney. Original data sheets from surveys by Tunbridge (1983) and McCarraher (1986a) were re-examined to collate previously unpublished data. The fish specimen collections from these surveys were also re-identified.

Nomenclature for fish species in the families from Petromyzontidae to Percidae (Table 1) follows Paxton et al. (1989), and for fish species in the families Gadopsidae to Eleotrididae follows Allen (1989).

Because of various limitations in data collected during 1967–1991 (e.g. non-standardised survey methodology, different species targeted and intermittent surveys), records from all surveys over the 24 year period were combined to produce general distribution maps for each species. The distributional information must be treated with caution, as during this period there has been considerable habitat modification in the region which may have changed species distributions and abundances considerably. The maps do, however, accurately reflect the current state of knowledge of the distribution of each species within the region.

SUMMARY OF MAJOR SURVEYS

Intensive inventory surveys of the fish fauna in East Gippsland have been conducted by the DCE. A few investigations which incidentally recorded fish species were conducted by other Government agencies or Universities (see Data Sources).

The first survey of fish assemblages in East Gippsland was a single, low intensity survey conducted in 1967 at two sites on the Combienbar River and at one site on the Cann River (B. R. Tunbridge, DCE, unpubl. data).

A limited survey at four sites in the upper Buchan and Suggan Buggan rivers during February 1974 was conducted by the then Fisheries and Wildlife Department (Dixon 1976; B. R. Tunbridge, DCE, pers. comm. 1991). In 1976 intensive netting surveys of estuarine and freshwater habitats at lower altitudes were started to determine the distribution of populations of commercially and recreationally exploited species. These surveys continued until 1983 but the distribution of smaller native fishes or of freshwater species in general was given little attention (McCarraher 1986a).

A survey involving sampling with the ichthyocide rotenone was conducted in the newly created Snowy River National Park in 1980, at two sites on the Snowy River and at one site each on the Deddick and Suggan Buggan rivers (B. R. Tunbridge, DCE, unpubl. data). Streams in the Croajingolong National Park were surveyed by mesh netting and rotenone sampling between 1980 and 1983, at 41 sites mostly in estuarine and low elevation fresh water habitats (Tunbridge 1983).

Low intensity surveys for commercially and recreationally exploited species were conducted in freshwater and estuarine habitats intermittently during 1979–1990 using mesh nets and rotenone (Baxter 1985, Baxter et al. 1989, 1991), and at four sites within the Croajingolong National Park in 1986 using electrofishing (B. R. Tunbridge, DCE, unpubl. data). A brief electrofishing survey of 31 freshwater sites in river basins 21 and 22 was conducted in 1988 (Koehn et al. 1991).

A survey conducted during February 1991 involved electrofishing and mesh netting at 18 sites in freshwater and estuarine habitats in the east of the East Gippsland river basin (S. R. Saddlier, DCE, unpubl. data). A further intensive survey of 23 sites in the Martins Creek Forest Block (Martin Creek/Brodribb River system) was conducted using electrofishing during May 1991 (S. R. Saddlier, DCE, unpubl. data).

The methods used to capture freshwater fish during 1967–1991 varied considerably. The use of rotenone was the main method utilised during earlier surveys, whereas electrofishing in shallow streams, and fyke and gill netting in deeper sections, were employed in later surveys. There were differences also in the capture efficiencies of the electrofisher units used in different surveys (see Koehn & McKenzie 1985).

The timing of the surveys has important implications in the apparent distribution and abundance of diadromous species. Surveys were conducted throughout most months of the year but the majority from late winter to late autumn (August though to May). This period includes the time of maximum diversity of diadromous species in freshwater habitats, during summer to early autumn (Koehn & O'Connor 1990b).

Family	Scientific name	Common name
NATIVE SPECIES		
PETROMYZONTIDAE	*Geotria australis* Gray, 1851	pouched lamprey
	Mordacia mordax (Richardson, 1846)	short-headed lamprey
ANGUILLIDAE	*Anguilla australis* Richardson, 1841	short-finned eel
	Anguilla reinhardtii Steindaehner, 1867	long-finned eel
CLUPEIDAE	*Potamalosa richmondia* (Macleay, 1879)	freshwater herring
RETROPINNIDAE	*Retropinna semoni* (Weber, 1895)	Australian smelt
PROTOTROCTIDAE	*Prototroctes maraena* Günther, 1864	Australian grayling
GALAXIIDAE	*Galaxias brevipinnis* Günther, 1866	broad-finned galaxias
	Galaxias maculatus (Jenyns, 1842)	common galaxias
	Galaxias olidus Günther, 1866	mountain galaxias
	Galaxias truttaceus Valenciennes, 1846	spotted galaxias
PERCICHTHYIDAE	*Macquaria novemaculeata* (Steindaehner, 1866)	Australian bass
KUHLIIDAE	*Nannoperca australis* Günther, 1861	southern pigmy perch
GADOPSIDAE	*Gadopsis marmoratus* Richardson, 1848	river blackfish
BOVICHTHYIDAE	*Pseudaphritis urvillii* (Valenciennes, 1831)	tupong
ELEOTRIDIDAE	*Gobiomorphus australis* (Krefft, 1864)	striped gudgeon
	Gobiomorphus coxii (Krefft, 1864)	Cox's gudgeon
	Philypnodon grandiceps (Krefft, 1864)	flat-headed gudgeon
	Philypnodon sp. nov.	dwarf flat-headed gudgeon
INTRODUCED SPECIES		
SALMONIDAE	*Oncorhynchus mykiss* (Walbaum, 1792)	rainbow trout
	Salmo trutta Linnaeus, 1758	brown trout
CYPRINIDAE	*Carassius auratus* (Linnaeus, 1758)	goldfish
	Cyprinus carpio Linnaeus, 1758	carp
PERCIDAE	*Perca fluviatilis* Linnaeus, 1758	redfin

Table 1. Scientific and common names of freshwater fish species recorded from East Gippsland during 1967–1991.

SURVEY SITES

Freshwater fish species have been recorded from 153 sites (Fig. 2) for which location data were available (see Appendix). Of these sites, 114 were located in freshwater reaches of streams and 39 in estuarine habitats. Many of the freshwater fish species in East Gippsland are diadromous and spend part of their lives in estuaries. Some species tolerate a wide range of salinity and are found naturally throughout the year in habitats ranging from estuarine to freshwater (Hart et al. 1989).

The number of freshwater survey sites for fish in East Gippsland is very small; by comparison, Jackson & Davies (1983) surveyed 115 sites in the Grampians region in an area 15% the size of East Gippsland, and Cadwallader (1979) surveyed 60 sites in one river system (Seven Creeks). Furthermore, most of the sites surveyed in East Gippsland are within the Snowy River and East Gippsland river basins; only one site (Lake Wau Wauka) has been surveyed in the Towamba River basin (McCarraher 1986a), and on one occassion.

FISH DISTRIBUTIONS

In contrast to other fish inventory surveys (Pusey et al. 1989, Hayes et al. 1989), the lack of standardised survey methodology between sites in East Gippsland, the low number of sites in specific river systems and the 24 year period over which the data were collected preclude analysis of the spatial variation in fish assemblages within or between river systems. Consequently, comments only on the gross distribution patterns of the freshwater fish species recorded from the three river basins (Table 1, Figs 3–9) are provided in the following sections.

Blyth & Jackson (1985) recorded 16 species of native and 3 species of exotic freshwater fish from East Gippsland; to these can now be added the native species *Geotria australis* (pouched lamprey), *Gobiomorphus coxii* (Cox's gudgeon) and *Philypnodon* sp. nov. (dwarf flat-headed gudgeon), and the exotic species *Perca fluviatilis* (redfin) and *Carassius auratus* (goldfish).

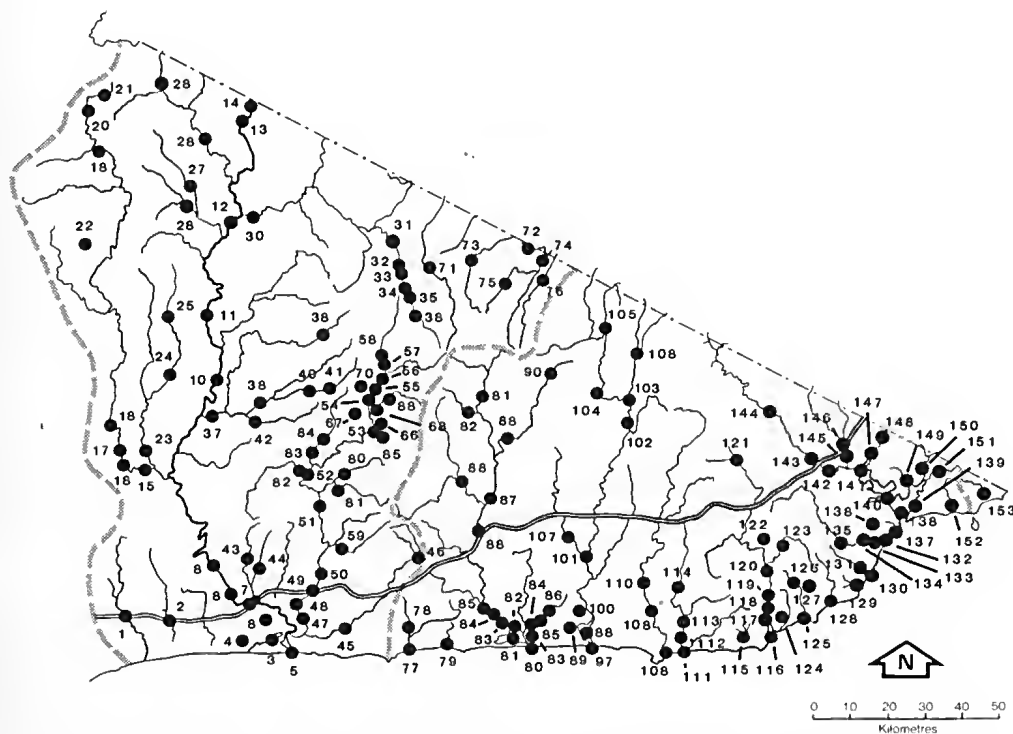Congeneric species of *Anguilla* (Fig. 4), *Gobiomorphus* (Fig. 8) and *Philypnodon* (Fig. 8) were

Fig. 2. Location map of survey sites for freshwater fish in East Gippsland during 1967–1991.

Species	No. of Sites	Abundance (No. of individuals)	Altitudinal Range (m)
Anguilla australis	78	115	0–1160
Pseudaphritis urvillii	68	446	0– 620
Galaxias maculatus	66	2736	0– 370
Anguilla reinhardtii	63	283	0– 320
Retropinna semoni	49	2008	0– 760
Salmo trutta	46	1049	0–1160
Philypnodon grandiceps	41	304	0– 370
Gadopsis marmoratus	39	279	10– 960
Macquaria novemaculeata	23	34	0– 200
Prototroctes maraena	20	80	0– 370
Nannoperca australis	16	136	0– 60
Mordacia mordax	16	275	30– 240
Galaxias brevipinnis	15	27	5– 320
Galaxias olidus	10	73	70–1320
Philypnodon sp. nov.	7	73	0– 20
Gobiomorphus australis	6	61	0– 50
Geotria australis	6	56	90– 220
Oncorhynchus mykiss	5	22	0– 840
Galaxias truttaceus	5	6	0– 100
Perca fluviatilis	3	5	720– 800
Gobiomorphus coxii	3	6	5– 50
Carassius auratus	2	11	6– 210
Potamalosa richmondia	1	1	0
Cyprinus carpio	1	?	0

Table 2. Occurrence, abundance and altitudinal range of freshwater fish species recorded from East Gippsland during 1967–1991.

found to occur sympatrically at many sites, as were the two monotypic genera *Geotria* and *Mordacia* (Fig. 3). The distribution of the four *Galaxias* species was less clear. At some sites *Galaxias maculatus* (common galaxias) occurred with one of the other three species, but *G. brevipinnis (broad-finned galaxias), G. olidus* (mountain galaxias) and *G. truttaceus* (spotted galaxias) occurred together only at one site (Wingan River, Fig. 6), where *G. maculatus* was also present. No native fish species are endemic to the region although five are restricted to Victorian coastal streams east of Wilsons Promontory: *Anguilla reinhardtii* (long-finned eel), *Potamalosa richmondia* (freshwater herring), *Macquaria novemaculeata* (Australian bass), *Gobiomorphus australis* (striped gudgeon) and *Gobiomorphus coxii* . A further three species are endemic to southern south-eastern Australia (Allen 1989): *Mordacia mordax* (short-headed lamprey), *Galaxias brevipinnis* and *Pseudaphritis urvillii* (tupong).

Native fish species

Geotria australis (pouched lamprey; Fig. 3). In Australia *G. australis* is a nocturnal species

inhabiting streams at low to high elevations (Merrick & Schmida 1984). Adults are rarely caught though downsteam migrants and ammocoetes may be seasonably abundant. In East Gippsland the distribution of the species is restricted and patchy (Table 2). The five sites found during an intensive survey of Martin Creek and Brodribb River in 1991 (S. R. Saddlier, DCE, unpubl. data) suggest that *G. australis* may be more widely distributed than previously thought, at least within the Snowy River basin. Past surveys may have misidentified *G. australis* ammocoetes as *Mordacia mordax*.

The Brodribb River is the most easterly extent of the recorded range for this species in Australia and represents a range extension. Previously, Paxton et al. (1989) recorded *G. australia* only as far east as Lake King, Gippsland.

Mordacia mordax (short-headed lamprey; Fig. 3). This species is nocturnal and commonly found as ammocoetes and adults in streams at low to high elevations (Merrick & Schmida 1984). In the Snowy River and East Gippsland basins it has been recorded from 16 sites at low to middle altitudes (Table 2). East Gippsland
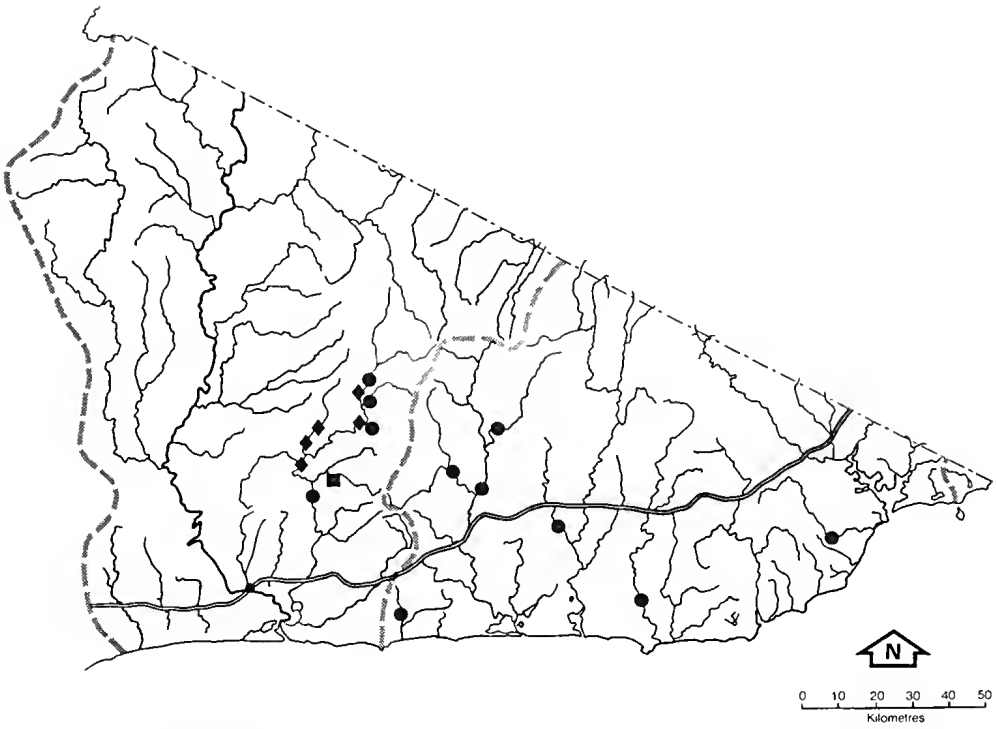
Fig. 3. Distribution of *Geotria australis* (■) and *Mordacia mordax* (●) in East Gippsland during 1967–1991. (♦) = both species.
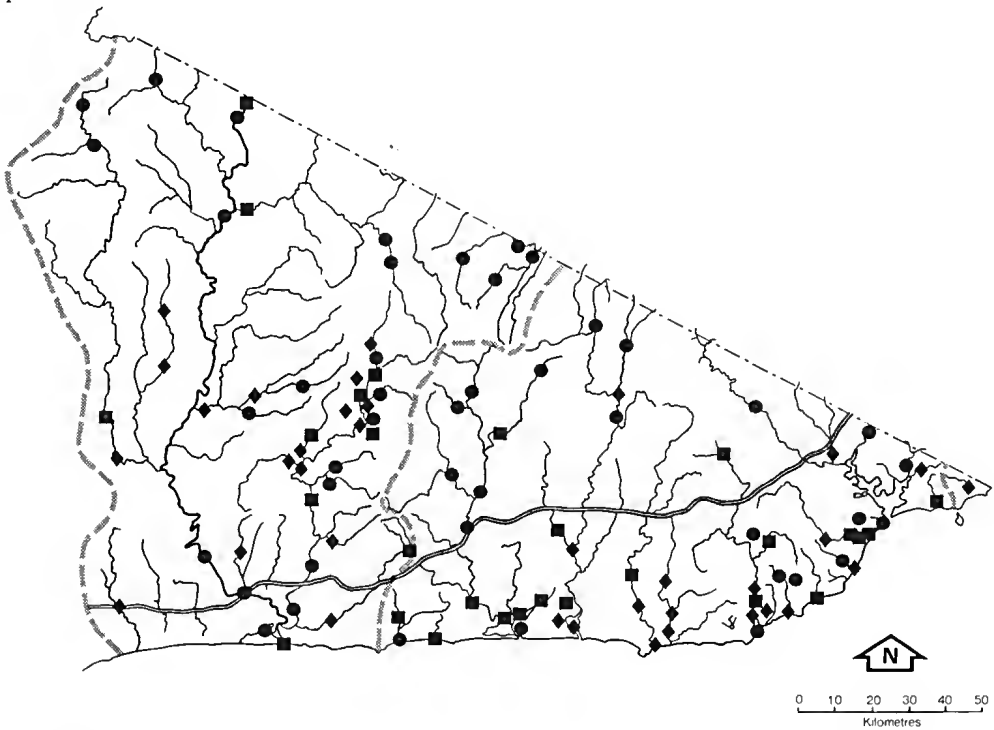

Fig. 4. Distribution of *Anguilla australis* (●) and *Anguilla reinhardtii* (■) in East Gippsland during 1967–1991. (♦) = both species.

T. A. RAADIK

falls within the middle of the geographical range of the species in Australia.

Anguilla australis (short-finned eel) and *Anguilla reinhardtii* (long-finned eel) (Fig. 4). Both these species were recorded from all three river basins and are common and widespread in East Gippsland where *A. australis* is the most widespread of all fish species, occurring at 78 sites (Table 2). *A. reinhardtii* was the fourth most widespread species (63 sites) and was found at low to middle elevations, whereas *A. australis* ranged higher into subalpine areas. Both species range northward along the New South Wales coast and westward across southern Victoria (Merrick & Schmida 1984). Survey data to support the record of *A. australis* from the Murrindal River by Tunbridge & Rogan (1981) were not located.

Potamalosa richmondia (freshwater herring; Fig. 5). One specimen of *P. richmondia* was collected together with 14 specimens of *Herklotsichthys castelnani* (southern herring) from Little River, Mallacoota Inlet in 1976. In the published report of the survey (McCarraher 1986a) the specimens of southern herring were incorrectly listed as freshwater herring. Other records of *P. richmondia* in Victoria (Cadwallader & Backhouse 1983) have not been substantiated. Paxton et al. (1989) recorded this species as far to the south-west as Lakes Entrance but survey data to support this record were not located. Elsewhere in Australia *P. richmondia* is distributed from estuarine environments to headwater streams (Pidgeon 1989).

Prototroctes maraena (Australian grayling; Fig. 5). This diadromous species can penetrate well inland from coastal areas if instream access is unrestricted (e.g. Craigie Bog Creek and Combienbar River, Fig. 5). *P. maraena* is patchily distributed in East Gippsland, having been recorded at 20 sites from low to middle elevations (Table 2) in two of the three river basins. Clear-flowing, gravel substrate streams suitable for *P. maraena* (see Jackson & Koehn 1988) do not appear to be present in the Victorian portion of the Towamba River basin.

Retropinna semoni (Australian smelt; Fig. 5). This salt-tolerant, non-diadromous species is the fifth most widely distributed species in East Gippsland, being found from low to high elevations and from all three river basins. The species
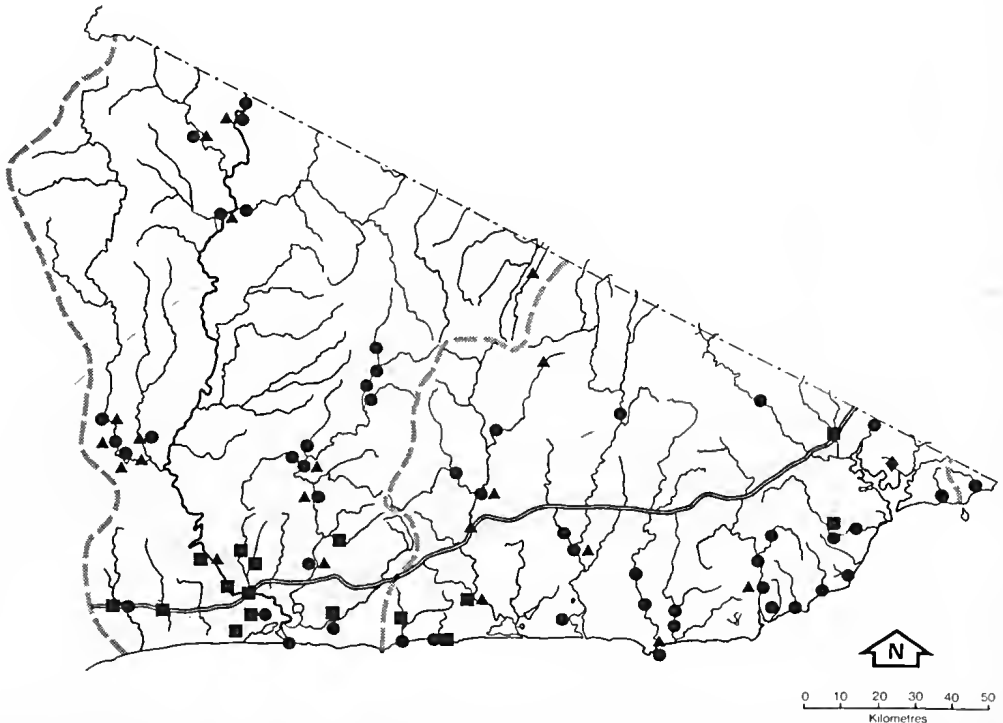

Fig. 5. Distribution of *Potamalosa richmondia* (♦), *Prototroctes maraena* (▲), *Nannoperca australis* (■) and *Retropinna semoni* (●) in East Gippsland during 1967–1991.

was recorded from 49 sites (Table 2), commonly in abundance.

Galaxias brevipinnis (broad-finned galaxias; Fig. 6). The distribution of this diadromous species is patchy throughout the Snowy River and East Gippsland river basins (15 sites), ranging from low to middle elevations (Table 2). The patchiness of the distribution probably reflects gaps in our knowledge rather than a restricted range in East Gippsland. The distribution in East Gippsland may extend also into upland areas as *G. brevipinnis* has been found elsewhere at high elevations (McDowall & Frankenberg 1981, Koehn & O'Connor 1990a). *G. brevipinnis* has been recorded from the New South Wales portions of the Genoa River (Llewellyn 1983), Wallagaraugh River (T. A. Raadik, DCE, unpubl. data) and upper Snowy River (McDowall & Frankenberg 1981), so that the species may also be considered present in the Victorian portions of these streams.

Galaxias maculatus (common galaxias; Fig. 6). This is the third most widespread species in East Gippsland, occurring at 66 sites ranging from sea level to middle elevations (Table 2). It is the only galaxiid species to be recorded from all three river basins and is a ubiquitous species in Victorian coastal streams. It is found elsewhere only at low elevations close to the coast (Cadwallader & Backhouse 1983).

Galaxias olidus (mountain galaxias; Fig. 6). In Australia this non-diadromous species is generally distributed from near sea level up to 1800 m (McDowall & Frankenberg 1981). In East Gippsland *G. olidus* is patchy in distribution, having been recorded from only 10 sites at low to high elevations (Table 2). Such patchiness may reflect gaps in our knowledge. Previously Blyth & Jackson (1985) recorded *G. olidus* in East Gippsland only from the Suggan Buggan River.

Galaxias truttaceus (spotted galaxias; Fig. 6). In East Gippsland this diadromous species has been recorded from the Snowy River and East Gippsland basins (Table 2) but only at five sites at low elevations, although it is common at low to middle elevations elsewhere in Australia (McDowall & Frankenberg 1981). Paxton et al. (1989) recorded *G. truttaceus* extending as far east as Wilsons Promontory, so that the range of
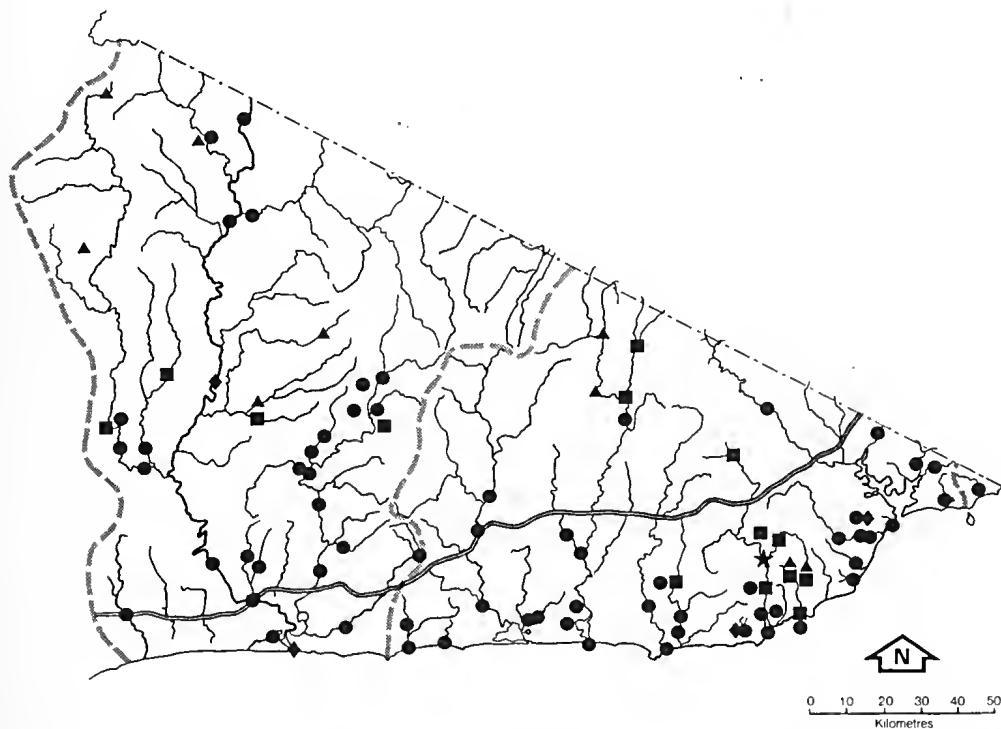

Fig. 6. Distribution of *Galaxias brevipinnis* (■), *Galaxias maculatus* (●), *Galaxias olidus* (▲) and *Galaxias truttaceus* (♦) in East Gippsland during 1967–1991. (★) = all four species.
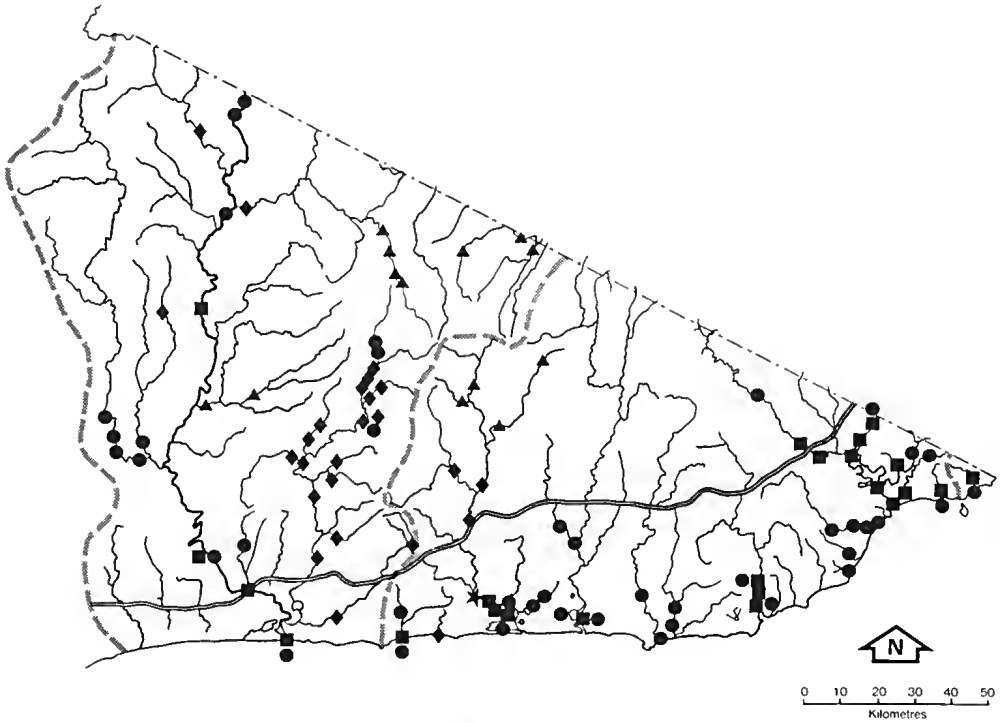
Fig. 7. Distribution of *Macquaria novemaculeata* (■), *Gadopsis marmoratus* (▲) and *Pseudaphritis urvillii* (●) in East Gippsland during 1967–1991. (♦) = G. *marmoratus* and P. *urvillii*, (★) = all three species.

the species should be amended to include all the Victorian coastal river basins in East Gippsland except basin 20. The most easterly known occurrence of *G. truttaceous* in Australia is in Sheep Station Creek (Betka River system, Fig. 1) but the species may extend into southern coastal New South Wales.

Macquaria novemaculeata (Australian bass; Fig. 7). In East Gippsland *M. novemaculeata* was recorded from 23 sites (ninth most widespread species) from low to middle elevations (Table 2). Elsewhere this species has been recorded from low to high elevations (Harris 1985), with males remaining in estuarine and lowland habitats after spawning and females predominating in lagoons or upland lotic habitats (Harris 1987). The lack of collection information for *M. novemaculeata* from middle to high elevations in the Snowy River and East Gipsland basins may be due to the species' seasonal abundance in freshwater, coupled with a lack of surveys in specific areas.

Survey data to support the records of this species by Tunbridge & Rogan (1981) from Thurra Swamp, Buchan River and the Brodribb River below and above the Princes Highway were not located.

Nannoperca australis (southern pygmy perch; Fig. 5). This species is distributed patchily (16 sites) throughout lowland East Gippsland (Table 2), though it has been found at middle elevations elsewhere in Victoria (Cadwallader 1979, Jackson & Davies 1983). *N. australis* prefers weedy, slow-flowing waters and therefore may be more widely distributed in the Snowy River and East Gippsland basins where available habitat exists. Maramingo Creek represents an eastward range extension for this species in coastal Victoria. Blyth & Jackson (1985) listed *N. australis* as occurring in the Red River but survey data to support this record were not located.

Gadopsis marmoratus (river blackfish; Fig. 7). This non-diadromous species is distributed widely throughout the Snowy River basin and extends eastward to the Bemm River system. It is the eighth most widely distributed species, being recorded from 39 sites from low to high altitudes (Table 2). It has not been recorded from the coastal river basins in southern New
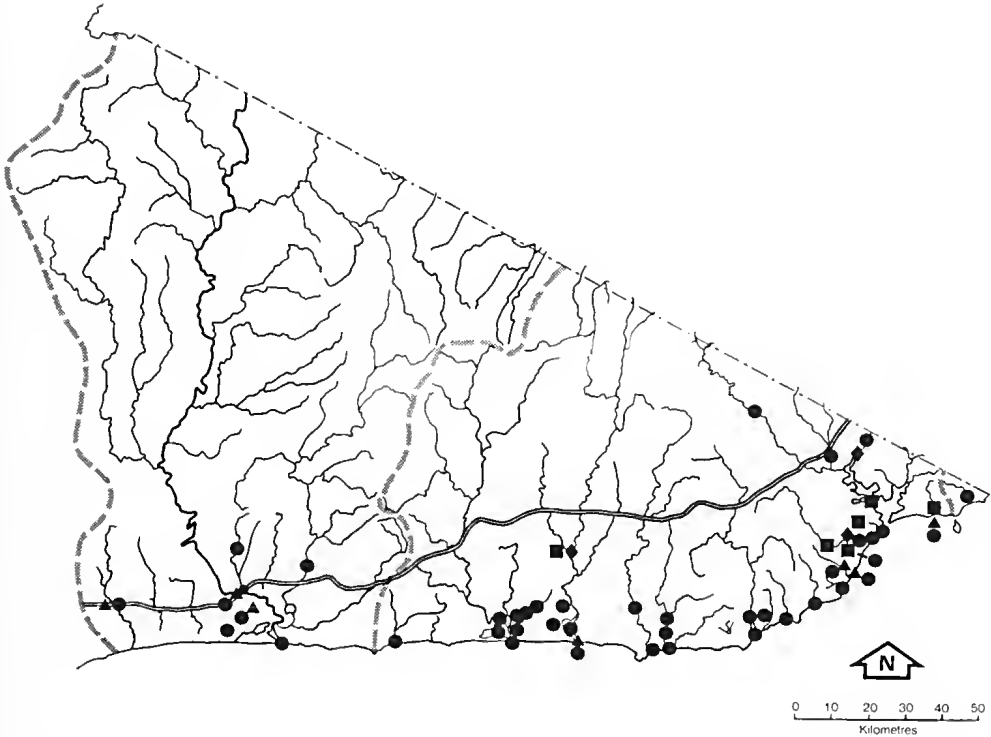
Fig. 8. Distribution of *Gobiomorphus australis* (■), *Gobiomorphus coxii* (♦), *Philypnodon grandiceps* (●) and *Philypnodon* sp. nov. (▲) in East Gippsland during 1967–1991.

South Wales (Llewellyn 1983, Allen 1989). Survey data to support the records of this species by Tunbridge & Rogan (1981) from the Little, Buchan and Murrindal rivers in the Snowy River system were not located.

G. *marmoratus* may be quite common within river systems in East Gippsland, as indicated by its presence in the Martin Creek and Brodribb River system in early 1991 (S. R. Saddlier, DCE, unpubl. data). Spencer et al. (1889) recorded *G. marmoratus* from Cabbage Tree Creek, from where it was most recently collected in 1989 (Koehn et al. 1991).

Pseudaphritis urvillii (tupong; Fig. 7). This species, the second most widely distributed in East Gippsland (68 sites), has been found from estuaries to the upper reaches of streams (Table 2) in all three river basins, and ranges farther eastward into the southern coastal drainages of New South Wales near Bega (Allen 1989).

Gobiomorphus australis (striped gudgeon; Fig. 8). This species appears to be restricted to coastal streams at low elevations. It has been recorded from only six sites in the Snowy River and East Gippsland basins (Table 2) but was

abundant and widespread in the Betka River in 1991 (S. R. Saddlier, DCE, unpubl. data). Elsewhere in Australia *G. australis* may be seasonally abundant and is more common at low elevations (Hoese et al. 1980). Cadwallader & Backhouse (1983) recorded this species from the lower Snowy River but survey data to support this record were not located.

Gobiomorphus coxii (Cox's gudgeon; Fig. 8). In East Gippsland this species is restricted to basin 21 (East Gippsland) where it has been recorded from only three sites at low elevations (Table 2), though elsewhere it is known to penetrate well inland to altitudes of 700 m. Further, *G. coxii* is often found in swiftly flowing streams and is rarely found at low altitudes near the ocean (Hoese et al. 1980). The distribution of *G. coxii* in Australia extends as far west as the Franklin River, South Gippsland (Cadwallader & Backhouse 1983).

Philypnodon grandiceps (flat-headed gudgeon; Fig. 8). This salt-tolerant, non-diadromous fish is the seventh most widely distributed species, ranging along coastal areas of East Gippsland

(41 sites) throughout the three river basins from low to middle altitudes (Table 2). Elsewhere in Victoria, *P. grandiceps* is often locally abundant (Cadwallader & Backhouse, 1983).

Philypnodon sp. nov. (dwarf flat-headed gudgeon; Fig. 8). This taxon was first recognised as being distinct from the closely related *Philypnodon grandiceps* by Hoese et al. (1980) but has remained formally undescribed. *Philypnodon* sp. nov. was first recorded from East Gippsland in 1972 when 56 individuals were collected from a tributary of the Snowy River (Department of Ichthyology, Australian Museum, Sydney, AMS 1.16969–17006). Further records from East Gippsland are scarce as little attempt has been made to distinguish this species from *P. grandiceps*.

Philypnodon sp. nov. is salt-tolerant and non-diadromous, and has been found from estuaries to elevations of a few hundred metres (Hoese et al. 1980). In East Gippsland specimens have been recorded from seven sites, all at low elevations (Table 2), but it is possible that some records of *P. grandiceps* from the region refer to *Philypnodon* sp. nov. It is regrettable that very few specimens from previous surveys were re-tained, as correct identifications could have been made retrospectively. *Philypnodon* sp. nov. may therefore be more widespead and abundant in all three river basins.

Introduced fish species

Oncorhynchus mykiss (rainbow trout; Fig. 9). A total of 268,990 individuals of *O. mykiss* were stocked into nine waters in the Snowy River basin between 1908 and 1969 (Barnham 1990). At present the species is confined to five sites in the Snowy River basin (Table 2), where specimens were recently recorded from the lower Snowy and Brodribb rivers and from the Bonang and Queensborough river systems. *O. mykiss* may have established self-sustaining populations in only a few higher altitude streams, with occasional specimens venturing downstream. Survey data to support records of this species from the Brodribb, Delegate, Snowy, Errinundra, Bemm and Combienbar rivers (Tunbridge & Rogan 1981) and from the Thurra and Cann rivers (Blyth & Jackson 1985) were not located. The population of *O. mykiss* in Beadle Lake has not been maintained by stockings since 1964.
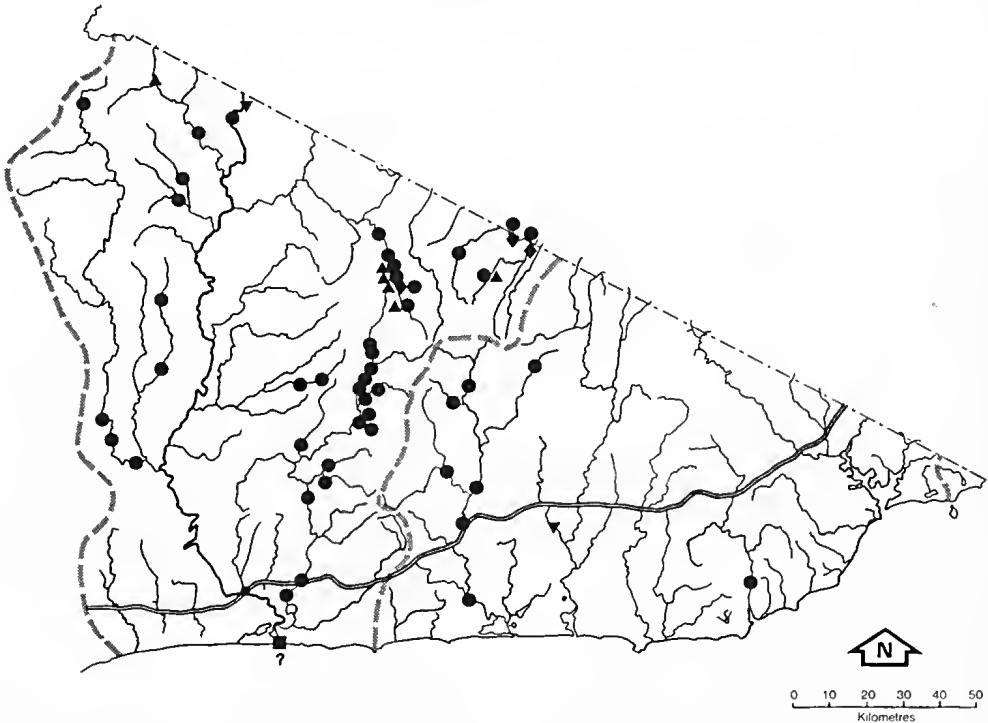

Fig. 9. Distribution of *Salmo trutta* (●), *Oncorhynchus mykiss* (▲), *Carassius auratus* (▼), *Cyprinus carpio* (■) and *Perca fluviatilis* (♦) in East Gippsland during 1967–1991.

Salmo trutta (brown trout; Fig. 9). A total of 160,885 individuals of this species were stocked into 13 waters in the Snowy River and East Gippsland river basins between 1889 and 1980 (Barnham 1990), and viable, self-sustaining populations are present throughout the Snowy River basin. *S. trutta*, the sixth most widely distributed species in East Gippsland (46 sites) ranges from low to high altitudes (Table 2) and eastward as far as the Bemm River system. Information from current surveys does not indicate whether the species is expanding its range farther eastward. Viable populations may be established in the Thurra River, and a single specimen was recently collected in the lower Wingan River (S. R. Saddlier, DCE, unpubl. data). Survey data were not located to support the records of this species from the Murrindal and Cann rivers and from below the falls at Sydenham Inlet (Tunbridge & Rogan 1981), and from the upper Thurra River (Blyth & Jackson 1985).

Carassius auratus (goldfish) and *Cyprinus carpio* (carp) (Fig. 9). There are no records of these two species having been stocked into waters in East Gippsland (C. Barnham, DCE, pers. comm. 1991). *C. carpio* was recorded from the lower Snowy River in 1971 (Malcolm 1971) but not since then. *C. auratus* has been recorded recently from one site each in the Snowy River and East Gippsland basins (Table 2), the Cann River system representing the eastern range extent of the species in southern Victoria.

Perca fluviatilis (redfin; Fig. 9). Self-sustaining populations of *P. fluviatilis* appear to be restricted to the cooler streams at high elevations in the Snowy River basin, namely the Bendoc, Queensborough and Bonang rivers (Table 2). Between 1950 and 1951 more than 2500 individuals of *P. fluviatilis* were stocked into Butchers Creek (Barnham 1990).

FAUNAL CHARACTERISTICS

Fish assemblages may be termed significant if they possess unique biological or conservation values, such as having an exceptionally high species diversity, containing threatened species or a unique combination of species, or being unaffected by the introduction of exotic species (Maitland 1985). Many sites in East Gippsland contain significant fish assemblages (see below, and Figs 3–9). The fish assemblages in streams east of the Bemm River system, including Doek Inlet and the Yeerung River (Fig. 1), are rated as significant because exotic species are generally

absent (Fig. 9; see also Macmillan 1990). Some other sites of particular significance are: the Rodger River at Waratah Flat, containing the largest known population of *Galaxias olidus* in East Gippsland; the Wingan River, containing all four species of *Galaxias* known from East Gippsland; the Little River (Mallacoota Inlet), the only known location for *Potamalosa richmondia* in East Gippsland; Elusive Lake, containing a land-locked population of the normally diadromous *Galaxias truttaceus*; and the Red River, a short coastal stream that is one of the few areas in the state where the non-diadromous species *Galaxias olidus* is found close to the ocean.

Since 1983, 24 pre-logging surveys have been conducted in East Gippsland to identify sites of significant flora and vertebrate fauna or significant habitats (Earl & Lunt 1989; S. Duncan, DCE, pers. comm. 1991). Regrettably no surveys included fishes, and consequently the distribution of significant freshwater fish species or assemblages has not contributed to forest management plans in the region to date.

Ten native fish species recorded from the region are considered threatened in Victoria (Table 3), and three of them, *Potamalosa richmondia, Prototroctes maraena* and *Macquaria novemaculeata*, are listed as threatened species under the Victorian *Flora and Fauna Guarantee Act 1988*. These 10 species represent 71% of the 14 threatened species found in Victorian coastal river basins (Koehn & Morison 1990). More significantly, these 10 species represent 70% of the diadromous species in East Gippsland, hence the importance of maintaining unobstructed instream passage for all stages of their life cycles. Two major rivers (Cann and Wingan) contain five threatened species, one (Snowy River) contains four species, and five systems (Barracoota Lake and Bemm, Brodribb, Buchan and Suggan Buggan rivers) each contain three threatened species. A maximum of three threatened fish species have been recorded from a single site (Figs 3–9).

Species diversity of freshwater native fish in East Gippsland is high, 19 of the 23 species known from coastal Victorian river basins (Koehn & O'Connor 1990b) having been recorded there. All of these 19 species except *Potamalosa richmondia* are found in the Snowy River basin, and all but *P. richmondia* and *Geotria australis* are found in the East Gippsland river basin. Only seven species (*Anguilla australis, A. reinhardtii, Retropinna semoni, Galaxias maculatus, Macquaria novemaculeata,*

Species	Conservation Status	Diadromous
Potamalosa richmondia	Endangered	*
Prototroctes maraena	Vulnerable	*
Geotria australis	Potentially Threatened	*
Galaxias brevipinnis	Potentially Threatened	*
Galaxias truttaceus	Potentially Threatened	*
Macquaria novemaculeata	Potentially Threatened	*
Galaxias olidus	Indeterminate	
Gadopsis marmoratus	Indeterminate	
Gobiomorphus australis	Indeterminate	*
Gobiomorphus coxii	Indeterminate	*
Philypnodon sp. nov.	Uncertain Status	
Mordacia mordax	Common	*
Anguilla australis	Common	*
Anguilla reinhardtii	Common	*
Retropinna semoni	Common	
Galaxias maculatus	Common	*
Nannoperca australis	Common	
Pseudaphritis urvillii	Common	*
Philypnodon grandiceps	Common	

Table 3. Victorian conservation status (from Koehn & Morison 1990) and diadromy (*) of native freshwater fish species recorded from East Gippsland during 1967–1991.

Pseudaphritis urvillii and *Philypnodon grandiceps*) have been recorded from the Towamba River basin. On a river system basis, diversity was highest in the Brodribb River (13 native species) followed by the Wingan River (11 species) (Figs 3–9). The Bemm, Betka, Cann and Buchan river systems had 10 species each, and a further six systems (Genoa, Mueller, Red, Yeerung rivers, and Cabbage Tree and Martin creeks) contained seven to nine species each.

Kinhill Engineers (1988), in discussing the depauperate fish fauna in Australian streams, stated that many Victorian native species are now restricted in distribution, and that consequently the number of native species in any given stretch of river is likely to be five or less. Six or more native species were present, however, at 26 sites in East Gippsland (Figs 3-9). One site (Brodribb River near the junction with Sardine Creek) had nine species, four sites (Betka and Wingan rivers and Martin Creek) had eight, 10 sites (Bemm, Betka, Cann, Thurra, Brodribb rivers and B. A., Cabbage Tree and Hospital creeks) had seven, and 11 sites (Wau Wauka Lake, Mueller, Red, Brodribb, Buchan, Suggan Buggan and Rocky rivers and Camp, Martin and Sardine creeks) had six species each.

Abundance data for all fish species at all sites in the three river basins were grouped to provide a gross indication of estimated numerical density during 1967–1991 (Table 2). *Galaxias maculatus, Retropinna semoni* and *Salmo trutta* were the most abundant species (more than 1000 individuals each), followed in decreasing order by *Pseudaphritis urvillii, Philypnodon grandiceps, Anguilla reinhardtii, Gadopsis marmoratus, Mordacia mordax, Nannoperca australis* and *Anguilla australis*, with abundances ranging from 446 to 115 individuals. Though *A. australis* was only the tenth most abundant species it was the most widely distributed, indicating that it occurs in low densities. *N. australis, M. mordax, Philypnodon* sp. nov. and *Gobiomorphus australis* were locally abundant but restricted in distribution. All threatened species (Table 3) except *Gadopsis marmoratus* were rare, with abundances of less than 100 individuals each. *S. trutta* is the only exotic species that was abundant and widely distributed; *Carassius auratus* was abundant (10 individuals) at one site only (Hall 1989).

Twelve of the 19 native species recorded from the region are diadromous (Table 3). The dominance of the fish fauna by these species is important in explaining distribution patterns throughout East Gippsland, because only five of the species (*Mordacia mordax, Geotria australis,*

Anguilla australis, A. reinhardtii and *Galaxias brevipinnis*) have the ability to traverse natural or man-made instream barriers (Koehn & O'Connor 1990a). The other seven species have limited or no ability to bypass barriers and may be absent upstream of an obstruction (see Hall 1989).

Of the non-diadromous species in the fauna (Table 3), *Galaxias olidus, Nannoperca australis, Gobiomorphus coxii* and *Philypnodon* sp. nov. are restricted in distribution and relatively low in abundance in East Gippsland. Coupled with their inability to migrate, these species are especially vulnerable because they have little ability to colonise new areas or to recolonise sites after local extinctions have occurred. Entire populations of non-diadromous species may be lost during catastophic events, such as wildfire and its after-effects on aquatic ecosystems (see Pescott 1983), or more gradual degradation of the instream habitat through loss of habitat, competition with exotic species or deteriorating water quality.

Water velocities and gradients, and the availability of suitable habitat, may also act to prevent the upstream movement of diadromous and non-diadromous fish species (Hayes et al. 1989).

The topography of East Gippsland ranges from low elevation, relatively narrow coastal plains, through dissected highlands to mountain areas which contain elevated plateaus in the north-west (LCC 1985, Macmillan 1990). As elevation increased the diversity of native fish species decreased (Table 2): 19 species at 0–100 m; 10 species at 101–400 m; five species at 400–700 m; and only two native species (*Anguilla australis* and *Galaxias olidus*) above 1000 m. Introduced species generally followed a similar pattern, with only *Salmo trutta* found above 1000 m. A similar trend in species diversity was observed by Lake & Fulton (1981), Pusey et al. (1989) and Hayes et al. (1989) in studies on fish assemblages in coastal streams in Tasmania, Western Australia and New Zealand respectively. This trend provides only a general guide to species diversity at particular elevations, because diversity at any locality depends on many factors such as land use, presence of exotic species, the size and depth of the stream, and environmental variables such as water velocity, gradient, depth and substrate (Taylor 1988, Hanchet et al. 1989, Hanchet 1990).

Further survey work in streams at altitudes of 200–800 m may increase the upper ranges where

the following species are recorded in East Gippsland: *Geotria australis, Mordacia mordax, Galaxias brevipinnis, G. truttaceus, Nannoperca australis, Gobiomorphus australis, G. coxii, Philypnodon grandiceps* and *Pseudaphritis urvillii.*

DISCUSSION

Sampling of fish in the freshwater habitats of East Gippsland has generally been spasmodic and the overall direction of surveys has been uncoordinated. Information obtained from successive surveys has not necessarily been complementary, so that gaps persist in our knowledge of species distributions. Most surveys have provided only general information on species distributions, and no attempt has been made to elucidate the distribution or habitat preference of fish species at various stages in their life cycles. In addition, no attempt has been made to determine trends in species distributions over time by establishing monitoring sites, a problem identified by the OCE (1989) in native fish research statewide.

Another limitation inherent in the distribution data is that most of the sites surveyed have been at easily accessible points, such as road crossings, where the riparian and instream habitat have been disturbed. It is not known whether fish assemblages at disturbed sites differ from those at unaltered sites; therefore assessments of species diversity or of numerical abundance at disturbed sites may not be reliable.

The distribution maps (Figs 3–9) consequently serve only as a general guide to fish distributions in East Gippsland. Due to the scarcity of data on species distribution in the region before 1967, it is difficult to know how closely the present day distributions mirror those of pre-European settlement, before the advent of land clearing, agriculture, mining and timber harvesting. It is also difficult to evaluate how species abundance and distribution changed with the advent of intensive timber harvesting in the 1960s (LCC 1985). The impact of exotic fish species on the native fish fauna is also unkown.

The distribution maps do, however, provide a benchmark from which to gauge future alterations in species distributions or changes in assemblages at specific sites. Fish are sensitive to changes in the aquatic environment and consequently are good indicators of environmental conditions (OCE 1989), especially those

species resident entirely in fresh water rather than the diadromous species. The maps also highlight the disjunct distribution of the many threatened species of native fish which inhabit the region, as well as those which have reached the limit of their range in East Gippsland.

The species list for East Gippsland (Table 1) may be expanded in the future if more intensive surveys are conducted. For example, the range of *Galaxiella pusilla* (dwarf galaxias) is known to extend to the Gippsland Lakes (Koehn et al. 1991) but may extend farther eastward into East Gippsland. Similarily, the ranges of *Hypseleotris compressa* (Empire gudgeon) and *Hypseleotris galii* (firetailed gudgeon) extend southwards into the New South Wales portion of the Towamba River basin (Llewellyn 1983, Allen 1989) and may extend into East Gippsland. *Mordacia praecox* (non-parasitic lamprey) is known with certainty only from the Tuross and Moruya rivers, south-eastern New South Wales (Allen 1989) but has been tentatively recorded from the La Trobe River system in Victoria (Harasymiw 1986, 1989). Consequently, this species may also be found in East Gippsland.

A notable feature of the fish fauna of East Gippsland is the low abundance (except for *Salmo trutta*) and diversity of exotic fish species, only five of the 12 exotic fish species known from Victorian fresh waters (OCE 1989) being recorded in the region. It is significant that *Gambusia holbrooki* (mosquitofish), widespread throughout Victoria (Cadwallader & Backhouse 1983), is absent from the region. Unconfirmed reports of its presence near Bairnsdale (J. Strong, Fisheries and Wildlife Protection Officer, Bairnsdale Region, pers. comm.) may indicate that the range of this species has expanded eastward from the MacAlister River (Hall 1989) and may extend into East Gippsland in the near future.

The natural significance of East Gippsland, identified by Blyth & Jackson (1985), has been further confirmed by the LCC (1991) which has proposed 10 major rivers and their tributaries as Victorian Heritage rivers, a further two rivers as Representative rivers and 16 catchments as Essentially Natural Catchments. Regrettably, except in the lower Bemm, Thurra and Snowy rivers, the Red and Benedore rivers, and Shipwreck, Easby and Seal creeks, few or no fish surveys have been conducted in these streams (Fig. 2).

There is therefore a pressing need for an immediate increase in coordinated fish survey effort in East Gippsland, with more intensive surveys conducted in more inaccessible reaches of streams and designed to complement existing knowledge of species distributions. The fish assemblages of many streams remain unsurveyed, and those in areas where freshwater habitats are under threat (e.g. forest coupes) should have first priority. Long-term population monitoring of these sites can provide useful data on the impact of the land-use practice on the component aquatic fauna.

Attention should also be directed to consolidating information on the abundance and distribution of threatened species, especially in middle elevation to upland areas of most river systems; to providing information on seasonal influences on the abundance and diversity of fish assemblages; and to the persistence of assemblages over time. The dominance of the native fauna by diadromous species makes it important to include information on the location of instream barriers when interpreting distribution patterns. Information on alterations to catchment land-use are also important as they may affect fish species distributions (Hanchet 1990).

CONCLUSION

Because the natural resources of East Gippsland are being increasingly exploited, information on species distributions and abundances of freshwater fish must be consolidated and enhanced. It must also be recognised that native freshwater fish are relevant to the scientific assessment of significant aquatic systems. Streams containing significant species or assemblages should be monitored for changes in species distributions over time, so that appropriate management strategies can be adopted to safeguard those ecosystems.

ACKNOWLEDGEMENTS

REFERENCES

ALLEN, G. R., 1989. *Freshwater Fishes of Australia.* TFH Publications, New Jersey.

ANDERSON, J. R. & MORISON, A. K., 1989. *Environmental Flow Studies for the Wimmera River, Victoria. Part B. Fish Habitat Assessment.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 74, Department of Conservation, Forests & Lands, Victoria.

ANON, 1974. Endangered native fish. *Victorian Fisheries and Wildlife Division, Freshwater Fisheries Newsletter* 7: 9–15.

AUSTRALIAN WATER RESOURCES COUNCIL, 1976. *Review of Australia's Water Resources 1975.* Australian Government Publishing Service, Canberra.

BARNHAM, C. B., 1990. Summary of researched available records of non-indigenous and indigenous fish stockings in Victorian public waters 1871 to 1990. Internal Operational Report No. 2, Fisheries Management Division, Department of Conservation and Environment. (On-going internal record, 4th edn.)

BAXTER, A. F., 1985. *Trout Management Group Fish Populations Surveys, 1978–1985; Location of Sampling Sites and Fish Species Caught.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 15, Department of Conservation, Forests & Lands, Victoria.

BAXTER, A. F., VALLIS, S. & BARNHAM, C., 1989. *A Summary of Trout Management Group Fish Population Surveys 1988.* Fisheries Management Report No. 27, Freshwater Fish Management Branch, Department of Conservation, Forests & Lands, Victoria.

BAXTER, A. F., VALLIS, S. & QUINLAN, P., 1991. *A Summary of Trout Management Group Fish Population Surveys 1990.* Fisheries Management Report No. 36, Inland Fisheries Management Branch, Department of Conservation and Environment, Victoria.

BELL, J. D., BERRA, T. M., JACKSON, P. D., LAST, P. R. & SLOANE, R. D., 1980. Recent records of the Australian grayling *Prototroctes maraena* Günther (Pisces: Prototroctidae) with notes on its distribution. *Australian Zoologist* 20: 419–431.

BLYTH, J. D. & JACKSON, P. D., 1985. The aquatic habitat and fauna of east Gippsland, Victoria. *Bulletin of the Australian Society for Limnology* 10: 89–109.

BRUMLEY, A. R., MORISON, A. K. & ANDERSON, J. R., 1987. *Revision of the Conservation Status of Several Species of Warmwater Native Fish after Surveys of Selected Sites in Northern Victoria (1982–1984).* Arthur Rylah Institute for Environmental Research Technical Report Series No. 33, Department of Conservation, Forests & Lands, Victoria.

CADWALLADER, P. L., 1979. Distribution of native and introduced fish in the Seven Creeks river system, Victoria. *Australian Journal of Ecology* 4: 361–385.

CADWALLADER, P. L. & BACKHOUSE, G. N., 1983. *A Guide to the Freshwater Fish of Victoria.* Victorian Government Printer, Melbourne.

CHESSMAN, B. C., 1971. Study of Victorian salt lake fishes with special reference to *Galaxias maculatus* (Jenyns, 1842) Pisces: Salmoniformes: Galaxiidae. BSc (Hons) thesis, Monash University.

DEPARTMENT OF CONSERVATION, FORESTS & LANDS, 1988. *Environmental Effects Statement. Proposed Trial of the Value Adding Utilisation System. Central Gippsland and East Gippsland Forest Management Areas.* Department of Conservation, Forests & Lands, Victoria.

DIXON, J. M. (ed.), 1976. Report on the Vertebrate Fauna of the Alpine Study Area of Victoria. Vertebrate Department, National Museum of Victoria, Melbourne.

DWR (DEPARTMENT OF WATER RESOURCES VICTORIA), 1989. *Water Victoria: An Environmental Handbook.* Victorian Government Publishing Office, Melbourne.

EARL, G. & LUNT, I., 1989. Bibliography of ecological survey reports, Department of Conservation, Forests & Lands, 1983 to August 1989. *Victorian Naturalist* 106: 205–207.

HALL, D. N., 1989. *Preliminary Assessment of Daily Flows Required to Maintain Habitat for Fish Assemblages in the La Trobe, Thomson, Mitchell and Snowy rivers, Gippsland.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 85, Department of Conservation, Forests & Lands, Victoria.

HALL, D. N., 1990. *Assessment of the Effects on Fish Habitat of Experimental Flow Releases for Hydropower Generation in the Tanjil River, Gippsland.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 109, Department of Conservation & Environment, Victoria.

HALL, D. N. & TUNBRIDGE, B. R., 1988. Distribution of native and introduced freshwater fishes in the Barwon River and its upper tributaries, Victoria. *Proceedings of the Royal Society of Victoria* 100: 61–65.

HANCHET, S. M., 1990. Effect of land use on the distribution and abundance of native fish in tributaries of the Waikato River in the Hakarimata Range, North Isalnd, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 24: 159–171.

HANCHET, S. M. & HAYES, J. W., 1989. *Fish and Fisheries Values of the Mokau River and Tributaries Draining the Mokau Goldfield.* Freshwater Fisheries Report No. 110, MAFFish, Christchurch, New Zealand.

HARASYMIW, B. J., 1986. *Fish Survey of Traralgon Creek.* Research and Development Department

Report No. SO/85/99, State Electricity Commission of Victoria.

HARASYMIW, B. J., 1989. *Fish Survey of the Morwell River and Biota Comparison with Traralgon Creek.* Research and Development Department Report No. SO/88/150, State Electricity Commission of Victoria.

HARRIS, J. H., 1985. Diet of the Australian bass, *Macquaria novemaculeata* (Perciformes: Percichthyidae), in the Sydney Basin. *Australian Journal of Marine and Freshwater Research* 36: 210–234.

HARRIS, J. H., 1987. Growth of the Australian bass, *Macquaria novemaculeata* (Perciformes: Percichthyidae), in the Sydney Basin. *Australian Journal of Marine and Freshwater Research* 38: 351–361.

HART, B. T., BAILEY, P., EDWARDS, R., JAMES, K., SWADLING, K., MEREDITH, C., MCMAHON, A. & HORTLE, K., 1989. Biological effects of saline discharges to streams and wetlands. A report to the Salinity Bureau. Centre for Stream Ecology, Chisholm Institute of Technology, Melbourne.

HAYES, J. W., LEATHWICK, J. R. & HANCHET, S. M., 1989. Fish distribution patterns and their association with environmental factors in the Mokau River catchment, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 23: 171–180.

HOESE, D. F., LARSON, H. K. & LLEWELLYN, L. C., 1980. Family Eleotridae. Gudgeons. In *Freshwater Fishes of South-Eastern Australia,* R. M. McDowall, ed., Reed Books, Sydney, 169–185.

JACKSON, P. D. & DAVIES, J. N., 1983. Survey of the fish fauna in the Grampians region, south-western Victoria. *Proceedings of the Royal Society of Victoria* 95: 39–51.

JACKSON, P. D. & KOEHN, J. D., 1988. *A Review of the Biological Information, Distribution and Status of the Australian Grayling (Prototroctes maraena* Günther), in Victoria. Arthur Rylah Institute for Environmental Research Technical Report Series No. 52, Department of Conservation, Forests & Lands, Victoria.

KINHILL ENGINEERS (PTY LTD), 1988. *Techniques for Determining Environmental Water Requirements — a Review.* Department of Water Resources, Victoria, Technical Report Series No. 40.

KOEHN, J. D., 1986a. *Western Port Catchment: Fishes, Their Habitats and Management Recommendations.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 40, Department of Conservation, Forests & Lands, Victoria.

KOEHN, J. D., 1986b. *Dandenong Creek: Fishes, Their Habitats and Management Recommendations.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 51,

Department of Conservation, Forests & Lands, Victoria.

KOEHN, J. D. & MCKENZIE, J. A., 1985. *Comparison of Electrofisher Efficiencies.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 27, Department of Conservation, Forests & Lands, Victoria.

KOEHN, J. D., MCKENZIE, J. A., O'CONNOR, J. P., O'CONNOR, W. G., O'MAHONY, D. J., RAADIK, T. A., SADDLIER, S. R. & TUNBRIDGE, B. R., 1991. *Miscellaneous Surveys of Freshwater Fish in Victoria: 1982–1990.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 110, Department of Conservation & Environment, Victoria.

KOEHN, J. D. & MORISON, A. K., 1990. A review of the conservation status of native freshwater fish in Victoria. *Victorian Naturalist* 107: 13–25.

KOEHN, J. D. & O'CONNOR, W. G., 1990a. The distribution of freshwater fish in the Otway region, south-western Victoria. *Proceedings of the Royal Society of Victoria* 102: 29–39.

KOEHN, J. D. & O'CONNOR, W. G., 1990b. *Biological Information for Management of Native Freshwater Fish in Victoria.* Victorian Government Printer, Melbourne.

LAKE, P. S. & FULTON, W., 1981. Observations on the freshwater fish of a small Tasmanian coastal stream. *Papers and Proceedings of the Royal Society of Tasmania* 115: 163–172.

LCC (LAND CONSERVATION COUNCIL), 1985. *Report on the East Gippsland Area Review.* Land Conservation Council, Victoria.

LCC (LAND CONSERVATION COUNCIL), 1991. *Rivers and Streams Special Investigation. Final Recommendations.* Land Conservation Council, Victoria.

LLEWELLYN, L. C., 1983. *The Distribution of Fish in New South Wales.* Australian Society for Limnology, Special Publication No. 7.

MACMILLAN, L., 1990. Conservation value and status of Victorian rivers. Part 2. East Gippsland rivers. Faculty of Environmental Design and Construction Research, Royal Melbourne Institute of Technology, Melbourne.

MAITLAND, P. S., 1985. Criteria for the selection of important sites for freshwater fish in the British Isles. *Biological Conservation* 31: 335–353.

MALCOLM, S., 1971. The status of common or European carp, *Cyprinus carpio,* in Victoria. BSc (Hons) thesis, Monash University, Clayton.

MCCARRAHER, D. B., 1986a. *Distribution and Abundance of Sport Fish Populations in Selected Victorian Estuaries, Inlets, Coastal Streams and Lakes. 1. Orbost Region.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 43, Department of Conservation, Forests & Lands, Victoria.

MCCARRAHER, D. B., 1986b. *Distribution and Abundance of Sport Fish Populations in Selected Victorian Estuaries, Inlets, Coastal Streams and*

Lakes. 2. Gippsland Region. Arthur Rylah Institute for Environmental Research Technical Report Series No. 44, Department of Conservation, Forests & Lands, Victoria.

McCarraher, D. B., 1986c. *Distribution and Abundance of Sport Fish Populations in Selected Victorian Estuaries, Inlets, Coastal Streams and Lakes. 3. Otway and Geelong Region.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 45, Department of Conservation, Forests & Lands, Victoria.

McCarraher, D. B., 1986d. *Distribution and Abundance of Sport Fish Populations in Selected Victorian Estuaries, Inlets, Coastal Streams and Lakes. 4. Portland Region.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 46, Department of Conservation, Forests & Lands, Victoria.

McDowall, R. M., 1988. *Diadromy in Fishes.* Croom Helm, London.

McDowall, R. M. & Frankenberg, R. S., 1981. The galaxiid fishes of Australia. *Records of the Australian Museum* 33: 443–605.

McKenzie, J. A. & O'Connor, W. G., 1989. *The Fish Fauna and Habitats of the Kororoit Creek, Truganina Swamp, Laverton Creek and Cherry Lake.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 97, Department of Conservation & Environment, Victoria.

Merrick, J. R. & Schmida, G. E., 1984. *Australian Freshwater Fishes: Biology and Management.* John R. Merrick, Sydney.

Morison, A. K. & Anderson, J. R., 1987. *Status of Trout Cod, Maccullochella macquariensis, Macquarie Perch, Macquaria australasica, and Other Fish Populations in the Upper Reaches of Seven Creeks, Based on Surveys Between 1981 and 1987.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 59, Department of Conservation, Forests & Lands, Victoria.

OCE (Office of the Commissioner for the Environment), 1989. *State of the Environment Report 1988. Victoria's Inland Waters.* Victorian Government Printer, Melbourne.

Paxton, J. R., Hoese, D. F., Allen, G. R. & Hanley, J. G., 1989. *Zoological Catalogue of Australia,* vol. 7, *Pisces. Petromyzontidae to Carangidae.* Australian Government Publishing Service, Canberra.

Pescott, T., 1983. Fish death after a flash flood in the Barwon River. *Geelong Naturalist* 20: 71–73.

Pidgeon, R. W. J., 1989. Age and growth of freshwater herring, *Potamalosa richmondia* Macleay (Clupeidae: Hyperlophinae), in the Bellinger River, New South Wales. *Australian Journal of Marine and Freshwater Research* 40: 679–692.

Pusey, B. J., Storey, A. W., Davies, P. M. & Edward, D. H. D., 1989. Spatial variation in fish communities in two south-western Australian river systems. *Journal of the Royal Society of Western Australia* 71: 69–75.

Ramm, D. C., 1986. An ecological study of the ichthyoplankton and juvenile fish in the Gippsland lakes, Victoria. PhD thesis, Univeristy of Melbourne.

Spencer, B. & French, C., 1889. Trip to Croajingolong. *Victorian Naturalist* 6: 1–38.

Taylor, M. J., 1988. *Features of Freshwater Fish Habitat in South Westland, and the Effect of Forestry Practices.* Freshwater Fisheries Report No. 97, MAFFish, Christchurch, New Zealand.

Timms, B. V., 1973. A limnological survey of the coastal lakes of East Gippsland, Victoria. *Australian Journal of Marine and Freshwater Research* 24: 1–20.

TIS, 1986. *Timber Industry Strategy.* (9). *Government Statement.* Victorian Government Printer, Melbourne.

Tunbridge, B. R., 1978. A survey of the fish populations in the Mitta Mitta River and tributaries before the construction of the Dartmouth Dam. In *Dartmouth Dams Project—Report on Environmental Studies,* State Rivers and Water Supply Commission for the River Murray Commission, 140 p.

Tunbridge, B. R., 1983. *Fish Populations in the Croajingolong National Park.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 9, Department of Conservation, Forests & Lands, Victoria.

Tunbridge, B. R., 1988. *Environmental Flows and Fish Populations of Waters in the South-Western Region of Victoria.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 65, Department of Conservation, Forests & Lands, Victoria.

Tunbridge, B. R. & Glenane, T. G., 1983. *Fisheries Value and Classification of Fresh and Estuarine Waters in Victoria.* Department of Conservation, Forests & Lands, Victoria.

Tunbridge, B. R. & Glenane, T. G., 1988. *A Study of Environmental Flows Necessary to Maintain Fish Populations in the Gellibrand River and Estuary.* Arthur Rylah Institute for Environmental Research Technical Report Series No. 25, Department of Conservation, Forests & Lands, Victoria.

Tunbridge, B. R. & Rogan, P. L., 1981. *A Guide to the Inland Angling Waters of Victoria,* 3rd edn. Government Printer, Melbourne.

APPENDIX

Location and altitude for each sample site. trib. = unnamed tributary, E = estuarine sites. **Map** number and grid reference correspond to 1:100,000 topographic survey map series.

Site no.	Watercourse	Basin no.	Map no.	Grid ref.	Altitude	
1	Hospital Ck	22	8522	048209	20	
2	Hartland R.	22	8522	123204	15	
3	Corringle L.	22	8522	310175	0	E
4	Beadle L.	22	8522	225163	10	
5	Snowy R.	22	8622	345154	0	E
6	Snowy R. trib.	22	8522	295218	10	
7	Snowy R.	22	8522	279245	5	E
8	Snowy R.	22	8522	230263	10	
9	Snowy R.	22	8522	210293	15	
10	Snowy R.	22	8523	199648	100	
11	Snowy R.	22	8523	190752	100	
12	Snowy R.	22	8523	248941	160	
13	Snowy R.	22	8524	264130	210	
14	Snowy R.	22	8524	268133	210	
15	Buchan R.	22	8522	078481	60	
16	Buchan R.	22	8523	034495	65	
17	Buchan R.	22	8523	034519	80	
18	Buchan R.	22	8523	036530	90	
19	Buchan R.	22	8524	003066	760	
20	Buchan R. trib.	22	8524	973159	1180	
21	Native Dog Ck	22	8524	006171	1320	
22	Moss Bed Ck	22	8523	961900	1030	
23	Murrindal R.	22	8523	085499	180	
24	Butchers Ck	22	8523	119653	320	
25	Butchers Ck	22	8523	118757	620	
26	Wulgulmerang Ck	22	8523	150966	780	
27	Little R.	22	8523	154997	720	
28	Suggan Buggan R.	22	8524	179095	370	
29	Suggan Buggan R.	22	8524	099191	680	
30	Deddick R.	22	8523	278937	200	
31	Bonang R.	22	8623	521888	640	
32	Bonang R.	22	8623	523854	680	
33	Bonang R.	22	8623	535810	680	
34	Bonang R.	22	8623	543805	720	
35	Bonang R.	22	8623	549795	720	
36	Bonang R.	22	8623	560766	820	
37	Rodger R.	22	8523	204588	120	
38	Rodger R.	22	8623	392724	680	
39	Yalmy R.	22	8523	276595	170	
40	Lt. Yalmy R.	22	8623	377627	360	
41	Lt. Yalmy R.	22	8623	410632	440	
42	Serpentine Ck	22	8523	268577	180	
43	Wall Ck	22	8522	264307	60	
44	Major Ck	22	8522	274283	15	
45	Cabbage Tree Ck	22	8622	543211	10	
46	Cabbage Tree Ck	22	8622	555317	145	
47	Curlip L.	22	8622	378205	5	E
48	Brodribb R.	22	8622	359233	5	
49	Brodribb R.	22	8622	383266	10	
50	Brodribb R.	22	8622	389301	15	
51	Brodribb R.	22	8622	388407	80	
52	Brodribb R.	22	8622	357479	90	
53	Brodribb R.	22	8623	488553	190	
54	Brodribb R.	22	8623	489623	220	

Site no.	Watercourse	Basin no.	Map no.	Grid ref.	Altitude	
55	Brodribb R.	22	8623	491631	240	
56	Brodribb R.	22	8623	506663	240	
57	Goongerah Ck	22	8623	509668	260	
58	Goongerah Ck	22	8623	501682	265	
59	Rocky R.	22	8622	428341	60	
60	Rich R.	22	8622	422473	140	
61	O'Connor R.	22	8622	423443	120	
62	Sardine Ck	22	8622	356479	90	
63	Martin Ck	22	8623	375509	140	
64	Martin Ck	22	8623	395536	180	
65	Big R.	22	8623	489552	190	
66	Fern Tree Ck	22	8623	488572	210	
67	Ironbark Ck	22	8623	460593	260	
68	B.A. Ck	22	8623	480585	210	
69	B.A. Ck	22	8623	504613	280	
70	Dead Calf Ck	22	8623	481615	220	
71	Delegate R.	22	8623	594848	860	
72	Bendoc R.	22	8623	764885	780	
73	Bendoc R.	22	8623	669870	960	
74	Queensborough R.	22	8723	797885	800	
75	Back Ck	22	8623	728837	840	
76	Craigie Bog Ck	22	8723	805856	760	
77	Yeerung R.	21	8622	559161	0	E
78	Yeerung R.	21	8622	558196	30	
79	Dock Inlet	21	8622	620167	0	E
80	Sydenham Inlet	21	9722	770168	0	E
81	Sydenham Inlet	21	8622	740180	0	E
82	Bemm R.	21	8622	749205	0	E
83	Bemm R.	21	8622	719215	10	
84	Bemm R.	21	8622	718217	10	
85	Bemm R.	21	8622	700228	15	
86	Bemm R.	21	8622	677358	70	
87	Bemm R.	21	8622	704439	100	
88	Goolengook R.	21	8622	642468	160	
89	Combienbar R.	21	8623	754544	200	
90	Combienbar R.	21	8723	802644	360	
91	Errinundra R.	21	8623	673594	200	
92	Ada R.	21	8623	674585	200	
93	Mud L.	21	8722	770185	0	E
94	Swan L. Channel	21	8722	770200	5	E
95	Swan L.	21	8722	786207	5	E
96	Swan L. trib.	21	8722	801221	10	E
97	Tamboon Inlet	21	8722	887166	0	E
98	Tamboon Inlet	21	8722	870200	0	E
99	Camp Ck	21	8722	863202	0	E
100	Furnell L.	21	8722	860231	10	E
101	Cann R.	21	8722	877304	50	
102	Cann R.	21	8723	947559	130	
103	Cann R.	21	8723	948615	160	
104	Cann R.	21	8723	903700	320	
105	Buldah Ck	21	8723	904725	340	
106	Fiddlers Green Ck	21	8723	948615	160	
107	Tonghi Ck	21	8722	854347	60	
108	Thurra R.	21	8722	018161	0	
109	Thurra R.	21	8722	991221	20	
110	Thurra R.	21	8722	975280	60	
111	Mueller R.	21	8722	046164	0	E
112	Mueller R.	21	8722	045181	0	E
113	Mueller R.	21	8722	042205	10	

Site no.	Watercourse	Basin no.	Map no.	Grid ref.	Altitude	
114	Mueller R.	21	8722	036278	110	
115	Elusive L.	21	8722	153194	40	
116	Wingan Inlet	21	8822	212193	0	E
117	Wingan R.	21	8722	197236	0	E E
118	Wingan R.	21	8722	196237	10	E
119	Wingan R.	21	8722	197254	40	
120	Wingan R.	21	8722	186336	70	
121	Wingan R.	21	8723	142503	160	
122	Wingan R. trib.	21	8722	190350	80	
123	Hard To Seek Ck	21	8822	217344	80	
124	Easby Ck trib.	21	8822	235218	60	
125	Red R.	21	8822	260218	0	
126	Red R.	21	8822	259274	100	
127	Red R. trib.	21	8822	271267	80	
128	Benedore R.	21	8822	310245	5	E
129	Seal Ck	21	8822	364278	0	E
130	Shipwreck Ck	21	8822	381296	0	E
131	Shipwreck Ck	21	8822	373297	20	
132	Betka R.	21	8822	420370	0	E
133	Betka R.	21	8822	400362	0	E
134	Betka R.	21	8822	372368	20	
135	Betka R.	21	8822	328352	50	
136	Sheep Station Ck	21	8822	400380	40	
137	Davis Ck	21	8822	428380	10	E
138	Mallacoota Inlet	21	8822	440420	0	E
139	Mallacoota Inlet	21	8822	470420	0	E
140	Mallacoota Inlet	21	8822	414435	0	E
141	Genoa R.	21	8823	363488	0	E
142	Genoa R.	21	8823	321485	5	E
143	Genoa R.	21	8823	290492	20	E
144	Genoa R.	21	8723	187596	100	
145	Maramingo Ck	21	8823	335507	20	E
146	Maramingo Ck	21	8823	333524	20	E
147	Wallagaraugh R.	21	8823	382523	5	E
148	Wallagaraugh R.	21	8823	403555	5	
149	Little R.	21	8823	452468	0	E
150	Dowell Ck	21	8823	478489	15	
151	Harrison Ck	21	8823	492481	20	
152	Barracoota L.	21	8822	525415	5	
153	Wau Wauka L.	20	8822	587445	5	

CONODONT DATA IN RELATION TO SEQUENCES ABOUT THE PRAGIAN–EMSIAN BOUNDARY (EARLY DEVONIAN) IN SOUTH-EASTERN AUSTRALIA

Ruth Mawson, John A. Talent, Glenn A. Brock and Michael J. Engelbretsen

School of Earth Sciences, Macquarie University, New South Wales 2109

Mawson, R., Talent, J. A., Brock, G. A. & Engelbretsen, M. J., 1992:09:30. Conodont data in relation to sequences about the Pragian–Emsian boundary (Early Devonian) in south-eastern Australia. *Proceedings of the Royal Society of Victoria* 104: 23–56. ISSN 0035-9211.

Conodont data are presented for the Cavan Formation at Wee Jasper in south-eastern New South Wales, and from stratigraphic sections and numerous spot samples and partial sequences through the Buchan Caves Limestone in its major outcrop tracts in eastern Victoria. Data from these areas and from Devonian sequences at Boulder Flat and Tabberabbera, Victoria, enable approximate alignments to be made with respect to the Pragian–Emsian boundary using as criterion the first appearance of *Polygnathus dehiscens* (overlapping with *P. pireneae*).

At Wee Jasper, the boundary is inferred to occur approximately 35 m below the "Cavan Bluff Limestone". Near-ubiquity of Ozarkodinan Biofacies (with absence or near-absence of polygnathids) hinders precise correlation of horizons within the Buchan Caves Limestone, but a scatter of records of *P. dehiscens* indicates that, except at Bindi, at least the upper half of the Buchan Caves Limestone, and perhaps substantially more, is early Emsian. Dearth or absence of conodonts from the dolomitic lower portion of the Buchan Caves Limestone in its various outcrop tracts leads to uncertainty regarding precise alignment of this widespread transgression. The Heath's Quarry carbonate buildup at South Buchan is argued to have continued upward growth long after the transgressive event reflected in the spreading of the pelagic Taravale facies over the Buchan Caves Limestone in the Buchan–Murrindal–The Basin area. At Bindi, following this last transgressive event, carbonate sedimentation continued; the Buchan Caves Limestone there ascends from the *dehiscens* Zone into the *perbonus* Zone. Samples from Boulder Flat and Tabberabbera indicate the presence of the latest Pragian *pireneae–trilinearis* interval, the productive samples at Tabberabbera including clasts in the basal unit, the Wild Horse Formation.

"*Spathognathodus*" *trilinearis* Cooper is assigned to *Polygnathus* and a new species, *Ozarkodina pseudomiae*, is described.

LIMESTONES of Early Devonian age are widespread in south-eastern Australia. Some are autochthonous, such as the Buchan, Wentworth and Murrumbidgee groups of the Buchan–Bindi, Tabberabbera and Taemas–Wee Jasper areas of south-eastern New South Wales and eastern Victoria (Fig. 1). Other limestone bodies such as those at Loyola, Deep Creek (east of Walhalla), Coopers Creek, Marble Creek (old Toongabbie marble quarries) and the Tyers–Boola areas of east-central Victoria are allochthonous (including isolated megaclasts) or interpretable as submarine fan deposits (Conaghan et al. 1976; Mawson, Talent et al. in prep.; J. A. Webb pers. comm.). Some of these were the focus of pioneering investigations on conodonts 20–25 years ago (Philip 1965, 1966; Philip & Jackson 1967; Philip & Pedder 1967a; Pedder et al. 1970; Cooper 1973) on the basis of which substantial changes in long-accepted stratigraphic alignments were profferred (e.g. Philip & Pedder 1964, 1967b, 1967c; Pedder 1967). Since then there have been major advances globally in understanding the sequence of conodont faunas through the Early Devonian and, with this improved knowledge, has come greater precision in making stratigraphic alignments.

A renewal of investigations into the Devonian conodont faunas of eastern Australia has so far focussed on sequences not including late Pragian or earliest Emsian horizons (Pickett 1978, 1980, 1984; Mawson 1986, 1987a, 1987b; Mawson & Talent 1989; Mawson et al. 1985, 1988). This was an interval during which major transgressive and regressive (T/R) events took place. Syntheses of stratigraphic data relative to Devonian T/R events have been presented (Talent 1969, 1989; Talent & Yolkin 1987). General accounts of Australian Devonian conodont biofacies have also been presented (Mawson et al.

Fig. 1. Location of principal Early Devonian sequences in south-eastern Australia including late Pragian–Emsian sequences investigated for this report.

1988: 513–521; Mawson & Talent 1989: 227) but, in the past two decades, no new conodont data have been provided for the interval about the Pragian–Emsian boundary. The extraordinarily low yields of generally nondescript conodonts obtained in early investigations of the Buchan Caves Limestone (Philip 1966) and Cavan Formation (Pedder et al. 1970) were uninviting. These low yields are clearly to be connected with very shallow environments, such as those represented by the dolomitic sequence at the base of the widespread Buchan Caves Limestone. These include intermittent supratidal environments indicated by fenestral fabrics. Nevertheless, in view of the excellent sections in so many areas, various south-eastern Australian sequences were deemed to have potential value for providing information not only on T/R events but on shallow water conodont biofacies as well.

The present investigation was initiated in response to an appeal from the International Subcommission on Devonian Stratigraphy for more data on conodont evolution about the Pragian–Emsian boundary. It had three other foci:

1. To provide a more precise date or dates for the major transgressive event (or events) indicated by the base of the Buchan Caves Limestone and by the Cavan Formation.

2. To attempt greater precision in stratigraphic alignment of various Pragian/Emsian limestone-bearing units in south-eastern Australia.

3. To obtain more information on the pattern of conodont biofacies at that time.

The following abbreviations are used for conodont genera throughout the text, on figures and tables: *A.* = *Amydrotaxis,* *B.* = *Belodella,* *D.* = *Drepanodus,* *E.* = *Eognathodus,* *I.* = *Icriodus,* *N.* = *Neopanderodus,* *O.* = *Oulodus,* *Pa.* = *Panderodus,* *Pand.* = *Pandorinellina,* *P.* = *Polygnathus.* Abbreviations used for stratigraphic sections are shown in Figs 2 and 3; additional abbreviations used in figure explanations are TAB for Tabberabbera and BF for Boulder Flat.

SEQUENCES INVESTIGATED: STRATIGRAPHIC BACKGROUND

1. *Cavan Formation*

The Taemas–Wee Jasper area is folded into a broad syncline–anticline–syncline system; the westernmost structure is the Wee Jasper Syncline. Three major Devonian units outcrop within it: the Black Range Group, a c. 2350 m sequence of subaerial to subaqueous acid volcanics and volcaniclastics, passing gradationally upwards into the c. 940 m Murrumbidgee Group (latest Pragian–Emsian), a carbonate sequence with subordinate clastics. The latter, in turn, passes gradationally into the Hatchery Creek Conglomerate, the transition taking place late in the Emsian within the *serotinus* Zone (Mawson & Talent, unpub. data). At least the last 70 m of the Taemas Formation is referable to the *serotinus* Zone (Philip & Jackson 1970, pl. 40, figs 6, 8; Ziegler 1977: 496). We are concerned here only with the Cavan Formation (Browne 1959; Cramsie et al. 1975, 1979; Owen & Wyborn 1979), the lowest unit of the Murrumbidgee Group.

In the Wee Jasper area, the Cavan Formation is gradational from the underlying Sugarloaf Creek Formation, a lithic sandstone–siltstone sequence. Three units are differentiated.

3 (highest). Unit C ("Upper Member"), consisting of mudstones with carbonates decreasing upwards, is 67 m in thickness on our measured section CABL (Figs 2C and 5) at Wee Jasper. The boundary with the overlying Majurgong Formation is gradational, being arbitrarily delineated by the last outcropping bed of limestone. At Cavan, in the Taemas area, the "Cavan Bluff Limestone" is overlain by "15 m of yellowish limestone with shale interbeds" followed by 7 m of massive limestone (Owen & Wyborn 1979), but there is no especially prominent limestone immediately above the "Cavan Bluff Limestone" (Unit B) at Wee Jasper. Other workers, therefore, might prefer to regard Unit C as being part of the Majurgong Formation, as was done by Pedder et al. (1970).

2. Unit B ("Middle Member") consists at Cavan of 9 m of laminated algal limestone overlain by 42 m of massive to well-bedded limestone (the "Cavan Bluff Limestone Member"). On our measured section CABL (Figs 2C and 5) at Wee Jasper there was only 18 m of massive limestone. Unit B is often highly fossiliferous and outcrops conspicuously.

1 (lowest). Unit A ("Lower Member") consists, in the Cavan area (Owen & Wyborn 1979), of 30 m of laminated grey and brown mudstones with minor, generally thinly bedded limestones. If, following Owen & Wyborn, we place the lower boundary of this unit at the first limestone, the thickness on our measured section CABL (Figs 2C and 5) at Wee Jasper is about 92 m.
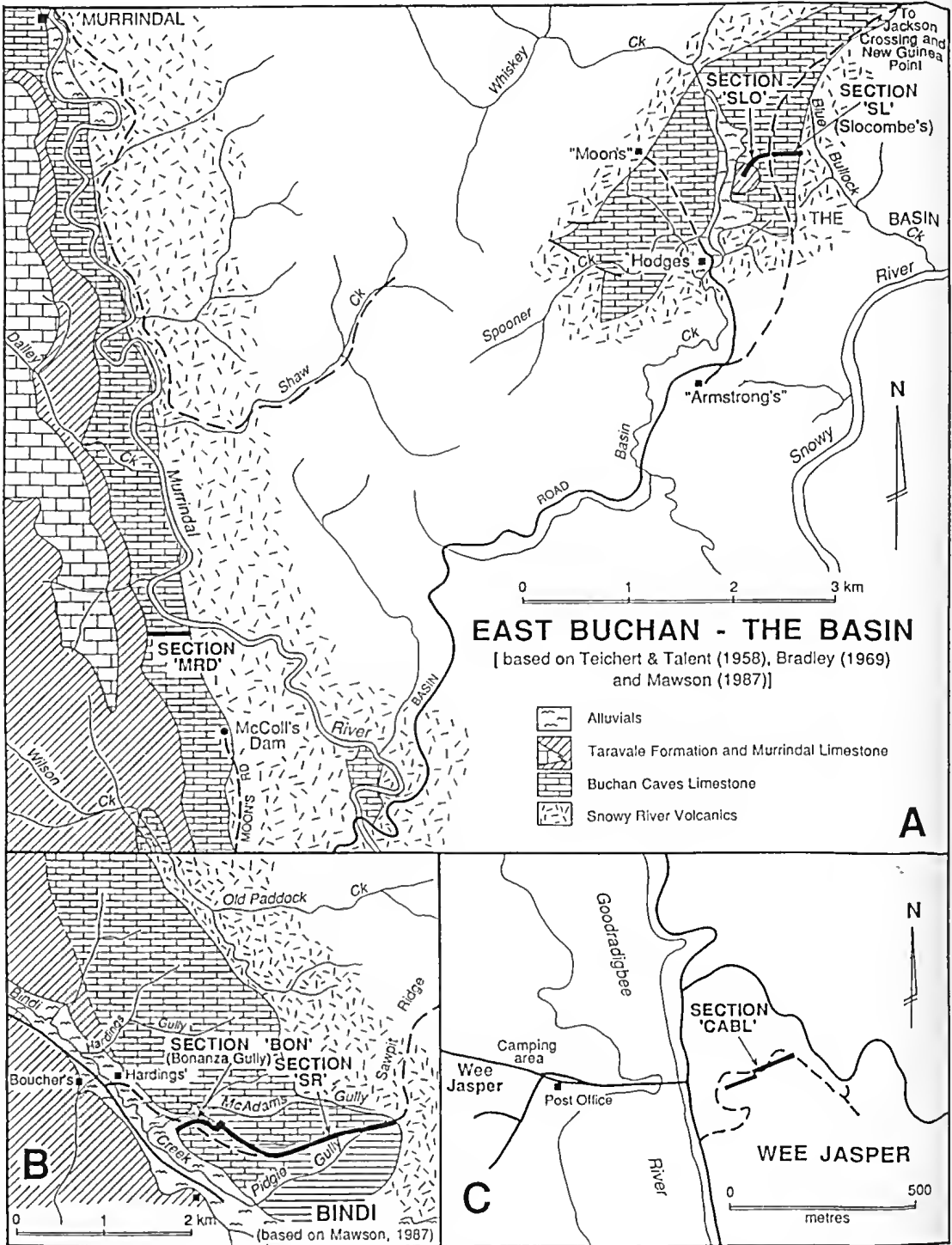
Fig. 2. A, the Buchan Group at The Basin and East Buchan showing location of sections sampled (prefixes SL and MRD). B, the Buchan Group at Bindi showing location of sections sampled (prefixes SR and BON). C, the Cavan Formation at Wee Jasper showing location of section sampled (prefix CABL).

2. *Buchan Caves Limestone*

The Buchan Caves Limestone (Talent 1956; Teichert & Talent 1958; Bradley 1969; Mawson 1987a) is a c. 210 m thick late Early Devonian transgressive carbonate unit structurally preserved in eleven significant and several tiny outcrop tracts in eastern Victoria (Fig. 1), principally in the Buchan–Murrindal, Bindi and Gillingal areas, at The Basin and in tracts along the Snowy River Valley and along Limestone Creek in the headwaters of the Indi River. Minimal thickness is about 67 m in the vicinity of the ruins of the former Slocombe homestead at The Basin; the maximum thickness measured was 236 m on our MRD section, but considerably thicker sequences are inferred to have existed in the Back Creek area of East Buchan.

The lower Buchan Caves Limestone consists generally of unfossiliferous dolomites and dolomitic limestones weathering to buff, dull grey or even earthy yellow with a characteristic pattern resembling criss-crossing knife incisions. This sequence is only 8 m thick in the outcrop tract near the junction of Dead Horse and Limestone creeks (Fig. 3A) but may exceed 35 m in the Back Creek area of East Buchan. The dolomitic sequence passes upwards into calcarenites and calcisiltites making up the bulk of the Buchan Caves Limestone. These tend to be monotonous and yield low-diversity faunas with brachiopods, almost invariably disarticulated and dominated by *Spinella* (Talent 1956). Apart from *Chalcidophyllum recessum* (Hill), occurring in abundance in a few beds, especially in the upper Buchan Caves Limestone, rugose corals are sparse. Tabulate corals, principally species of *Favosites, Syringopora* and *Thamnopora*, tend to be more common and diverse (Hill 1950). Oncolitic horizons in this sequence at Buchan (Talent 1956) and Bindi, coupled with absence of bryozoans, trilobites and even a dearth of molluscs, except for small nondescript forms tending to occur as nuclei of oncoliths, are consistent with very shallow water, abnormal as regards circulation and/or salinity.

More diverse faunas occur in the uppermost third of the Buchan Caves Limestone. Occasional horizons, usually dark grey calcilutites and calcisiltites, have produced abundant ostracodes (Krömmelbein 1954), bivalves (Talent 1956; P. A. Johnston, unpub.), bellerophontids and occasional cephalopods (Teichert & Glenister 1952).

Diverse silicified faunas have been found in two areas: a gastropod–bivalve fauna near the top of the Buchan Caves Limestone in the vicin-ity of Slocombe's Cave at The Basin; and a rather diverse brachiopod fauna near the top of the formation on the ridge extending eastwards from Chisholm homestead, about 1.8 km south of Murrindal. Such relatively high diversity faunas are exceptional departures from the prevailing low diversity believed to have been connected with very shallow marine conditions that extended regionally (the Buchan–Indi–Combienbar Shelf of Talent 1969).

The Buchan Caves Limestone is a notably high purity carbonate sequence. Local developments of shales, calcareous mudstones and nodular limestones have been noted in excavations made during fencing in Spooner Creek, The Basin, and were formerly well-expressed in low road cuttings on the Buchan–Orbost road about 1.2 km south-east of the Back Creek bridge. The last of these, focus of Talent's (1956) Cameron Member, was largely obliterated by road realignment in the late 1960s. It had been interpreted (mapping by V. N. Cottle, in Teichert & Talent 1958) as a fault-bounded sliver of Taravale Formation. These two occurrences produced well-preserved brachiopod–coral faunas with an abundance of ostracodes in the latter. Such occurrences were obviously rare in the otherwise monotonous carbonate platform.

The most substantial developments of high diversity brachiopod faunas with high articulation-index occur in what we have previously referred to (Mawson 1987a; Talent & Yolkin 1987; Talent 1989) as the upper Buchan Caves Limestone at Bindi, especially in Pidgie, Bonanza and McAdam's gullies (for localities see Mawson 1987a, Fig. 3) in a distinctive, recessive, thinner bedded, occasionally argillaceous unit high in the *dehiscens* Zone, overlain by a unit of more thickly bedded limestones. We have inferred the thinner bedded sequence to reflect a deepening or transgressive event (Talent & Yolkin 1987; Talent 1989), corresponding to the transgressive event at Buchan expressed as the abrupt change from Buchan Caves Limestones to Taravale Formation mudstones and nodular limestones characterized by pelagic faunas—dacryoconarids, ammonoids (rare) and conodonts typical of the Polygnathid Biofacies.

Webb (1992) has suggested extending use of the term Murrindal Limestone into the Bindi area, applying it to a unit we informally referred to as the "Shanahan Limestone" (Mawson 1987) and to the upper of the two transgressive cycles we discriminated within what we have previously referred to as the Buchan Caves Lime-
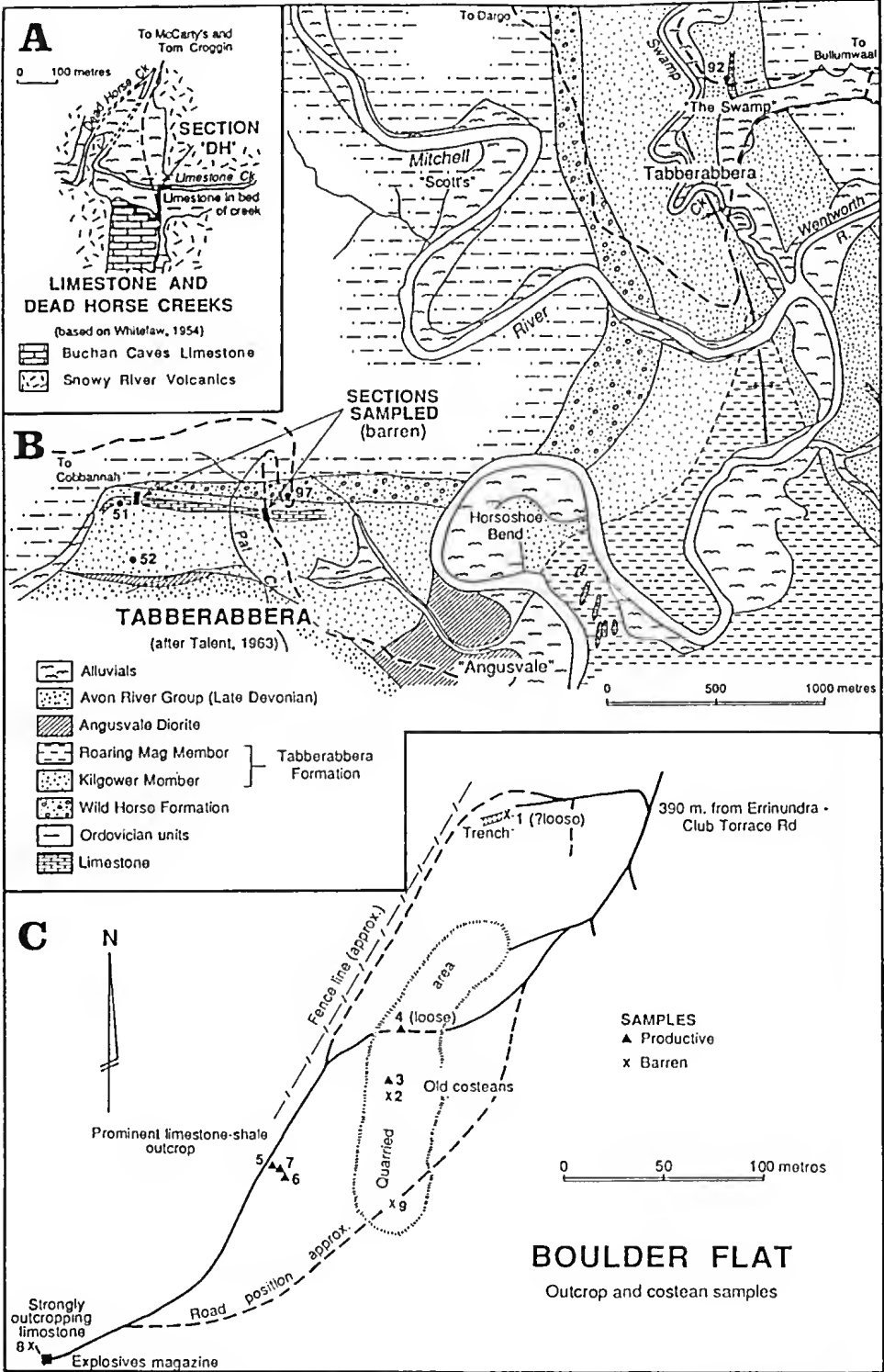
Fig. 3. A, the Buchan Group at the junction of Dead Horse and Limestone creeks showing section sampled (prefix DH). B, location of stratigraphic sections (both barren) and productive spot samples at Tabberabbera (prefix TAB). C, location of spot samples at Boulder Flat (prefix BF).

stone at Bindi. We believe Webb's suggestion to have merit, particularly as we now know that the northern part of the Buchan Group at Bindi is fundamentally synclinal and that the "Shanahan Limestone" is a repeat by folding of the uppermost part of the Buchan Caves Limestone (or Murrindal Limestone *sensu* Webb), truncated to the west by the Indi Fault.

Spot sampling by Philip (1966) of the Buchan Caves Limestone for conodonts at Buchan some 25 years ago gave disappointing results; no polygnathids were obtained. Since then the conodont faunas of the uppermost part of the Buchan Caves Limestone at Bindi and beds about the Buchan Caves Limestone–Taravale Formation boundary at Murrindal have been documented (Mawson 1987a), but there are no published data on the sequence of conodonts through the rest of the Buchan Caves Limestone.

3. *Loyola*

Conodonts have been described using single-element taxonomy (Cooper 1973) from four limestone bodies outcropping at Loyola, 11 km south-west of Mansfield and 200 km north-east of Melbourne. The faunas are significant as they include four specimens of a form, *"Spathognathodus" trilinearis*, recognized as new by Cooper, as well as two incomplete and poorly preserved specimens of *Polygnathus* not specifically identified by him but thought to be probably *P. dehiscens*. As noted below, we believe the latter two specimens more likely to be *P. pireneae* Boersma; we refer *"S". trilinearis* also to *Polygnathus*, believing it to be good evidence for derivation of the genus from *Eognathodus*.

The specimens of *P. trilinearis* (Cooper) and *P. pireneae* were not obtained from the same lens. The former came from a 36 kg sample from the quarry at the Old Lime Kiln, about 750 m north-west of, and conceivably stratigraphically beneath, the limestones outcropping in Griffiths's Quarry, the source of the specimens of *P. pireneae*. The area has few and generally poor outcrops. Despite this, the geometry of a belt of fossiliferous grits and conglomerates outcropping c. 500 m south-west of the quarries (Cooper 1973, fig. 1) indicates that the matrix of the two limestone occurrences, as well as that of the Cummins Road limestone outcrop, may be assumed to be stratigraphically equivalent or very nearly so. The limestone lenses, however, may be olistoliths (Conaghan et al. 1976: 529) and thus conceivably divergent in age. We cannot be sure, therefore, from previously available information from Loyola, whether the time-range of *P. trilinearis* overlaps with that of *P. pireneae*.

4. *Boulder Flat*

Limestones overlying a mixed volcanic-sedimentary succession were reported by Thomas (1949) from Boulder Flat in the Errinundra valley, 15.1 km by road north of Club Terrace in eastern Victoria. The outcrops about Boulder Flat were examined by one of us [JAT] in 1954. The marine sediments below the limestones, shown by Thomas (1949, loc. 3) as containing *"Tentaculites* and spirifers, etc.", produced *Spinella* too badly sheared for specific identification but bearing the spinose microsculpture characteristic of the genus. Poorly preserved favositids, rugose corals and cross-sections of brachiopods consistent with *Buchanathyris* and *Spinella* but too badly preserved for generic identification were obtained from the limestones. Thomas's correlations were therefore accepted (Talent 1965) but were subsequently challenged (Ramsey & VandenBerg 1986) on lithological grounds and on the basis of identifications (Pickett 1984) of the conodonts *Amydrotaxis druceana* (Pickett) and *"Delotaxis" tenuistriata* Pickett from the limestones. The entire volcanic–sedimentary sequence was referred to as the Errinundra Group (Ramsey & VandenBerg 1986; VandenBerg 1988; VandenBerg et al. 1990) and interpreted (VandenBerg 1988) as a "structural remnant of a small rift-like extensional basin in which shallow marine sedimentation was contemporaneous with silicic volcanism". The Errinundra Group was viewed as consisting of two formations: the Bungywarr Formation below overlain by the Boulder Flat Limestone. The former was construed as consisting of two members: the Blackwatch Volcaniclastic Member above and the Bola Sandstone Member below.

The limestones at Boulder Flat are dolomitic, mineralized (barite and sulphides) and often extremely recrystallized and stylobrecciated. Outcrops are poor and have been made worse by bulldozing for barite. Unaware that work was being undertaken by VandenBerg (in Pickett 1984), we repeatedly sampled the limestone area at Boulder Flat (Fig. 3C) in the early 1980s.

5. *Waratah Bay*

The Bell Point Limestone (Fig. 4), outcropping in three areas on the west side of Waratah Bay, Victoria, has been correlated with the Buchan Caves Limestone and inferred to be an expression of the same transgressive event (Talent
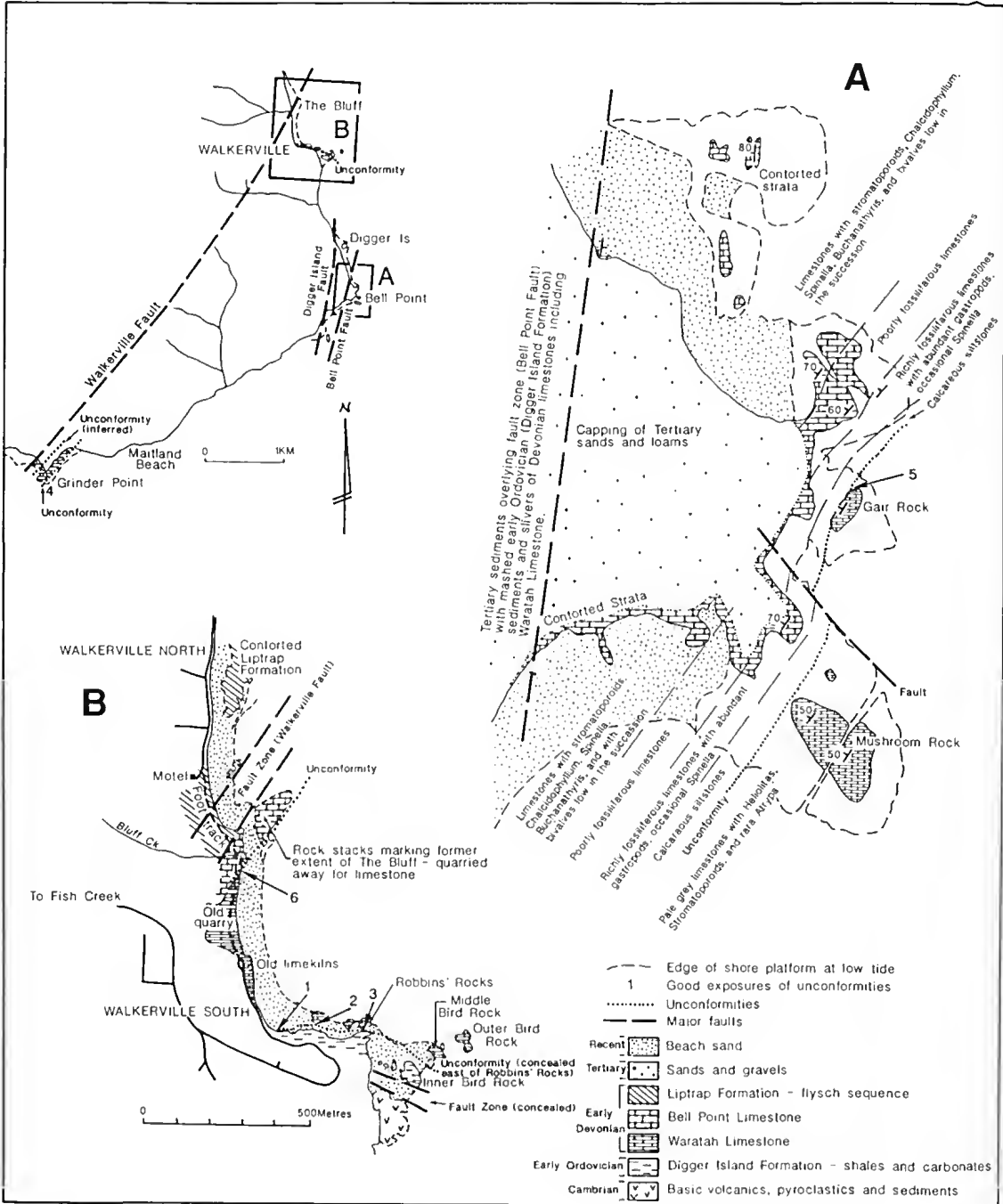
Fig. 4. Early Devonian carbonate units and unconformities on the west side of Waratah Bay (from Talent 1989, fig. 5, with corrections; based on Talent 1955). Points 1–3 are areas where the unconformity between the Bird Rock Member of the Waratah Limestone and strongly jointed dolomites of the Early Ordovician Digger Island Formation is well expressed. At point 4 the same unconformity, but of Waratah Limestone on a Cambrian volcanic–sedimentary succession, is superbly expressed. Point 5 shows the unconformity between the Bell Point and Waratah limestones.
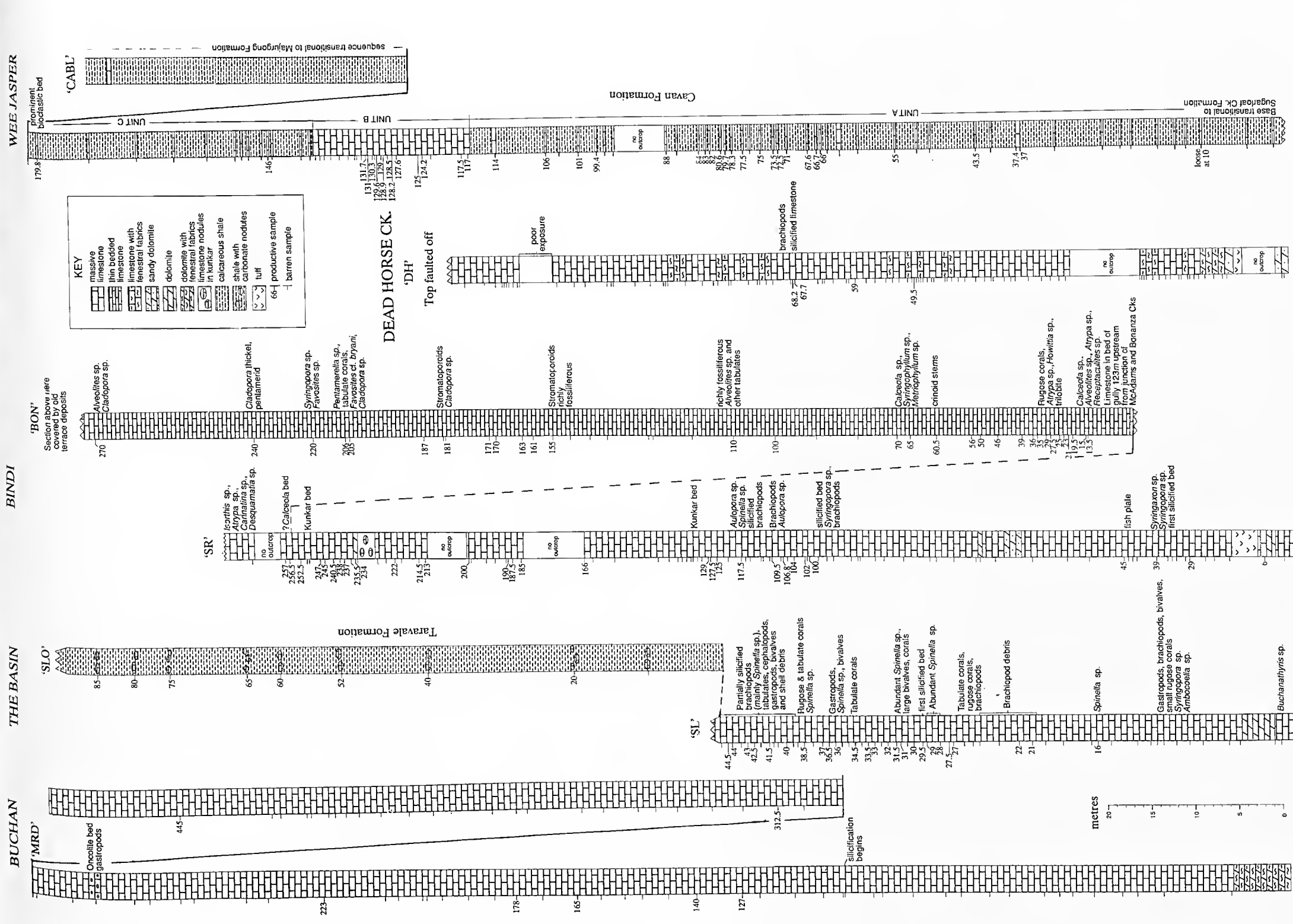
Fig. 5. Stratigraphic sections through the Buchan Group, principally Buchan Caves Limestone, at East Buchan (MRD section), The Basin (SL and SLO sections), Bindi (SR and BON sections), Dead Horse Creek (DH section) and through the Cavan Formation at Wee Jasper (CABL section).

1955, 1965, 1989). The limestones at Waratah Bay were sampled for conodonts by J. C. Argent (1971) within the framework of Talent's (1955) unpublished mapping. Of Argent's samples, 81 proved productive, 36 yielding forms of *Eognathodus*; most others yielded forms of no great correlative significance, and numerous samples were barren. A brief comment was made on some of Argent's identifications by Talent (1989). As a published version of Argent's dissertation has now appeared (Bischoff & Argent 1990), additional comment follows.

1. Talent (1955, 1965, 1989) differentiated between the Waratah Limestone and the unconformably overlying Bell Point Limestone, the former including the Bird Rock and Kiln Members proposed by Teichert (1954). When originally proposed, the Bird Rock Member included a poorly bedded, strongly jointed, pale grey dolomitic sequence outcropping on the foreshore cliffs behind Robins' Rocks [= Robin Rock of Bischoff & Argent]. Despite lack of fossil evidence (samples we have taken for conodonts have proved barren), this sequence is now referred on lithological grounds to the Early Ordovician Digger Island Formation (Talent 1989). The angular unconformity between it and the overlying orange-buff basal sequence of the lower Waratah Limestone is clearly displayed as a thin, basal, pebbly interval. If this restriction in definition is accepted, and it was the fossiliferous section that was clearly intended by Teichert (1954, and in Hill 1954) for his Bird Rock Member, Bischoff & Argent's (1990) "Lower Grinder Member" is more or less a synonym.

2. The unconformity at the top of Bischoff & Argent's (1990) "Mushroom Rock Member", beautifully expressed on the west flank of Gair Rock at Bell Point (Talent 1955, 1965, 1989) is, for us, the same unconformity as the one readily identifiable at the top of Teichert's Kiln Member in the coastal section between Walkerville South and Walkerville North (see Fig. 4). Bischoff & Argent's "Mushroom Rock Member" is therefore an approximate synonym of Teichert's Kiln Member.

6. *Tabberabbera*

The Wentworth Group is a predominantly elastic Early Devonian sequence outcropping in the watersheds of Sandys Creek and the Wentworth and Mitchell rivers in east-central Victoria (Talent 1963). The profound angular unconformity at Tabberabbera between the marine Early Devonian Wentworth Group and the nearly flat-lying non-marine Late Devonian Avon River Group is the typical expression of what has long been termed the Tabberabberan Orogeny (Andrews 1938; Talent 1963, 1965). Talent (1963) suggested that the youngest unit of the Wentworth Group, the Roaring Mag Member of the Tabberabbera Formation, could be approximately correlative with the Buchan Caves Limestone; the underlying Kilgower Member of the Tabberabbera was believed to be significantly older.

INTERPRETATION OF CONODONT DATA

To obtain the results presented here, more than 5 tonnes of samples were collected, mostly along measured stratigraphic sections (Fig. 5), and were partially acid-leached; the sources of 551 of these samples and their productivities are listed in Table 1. Positions of stratigraphic sections are shown in Figs 2 and 3. Positions of horizons sampled, productive and barren, are indicated on the stratigraphic columns in Fig. 5, with additional information for the BON section, particularly offsets, shown in Fig. 6.

Among the numerous 5–10 kg spot samples were a c. 200 kg sample from McColl's Dam, east of Buchan (Fig. 2A) and c. 100 kg samples from localities 92 and 97 at Tabberabbera (Fig. 3B) and from the limestone at the junction of Sandys Creek and the Mitchell River (Easton 1938; Talent 1963), 6 km south of Tabberabbera. In general, samples that proved barren after leaching 1 or 2 kg were not subjected to further

LOCALITY	Number of samples taken	No. of samples with conodonts
CABL stratigraphic section	81	39
SL stratigraphic section	58	25
SR stratigraphic section	91	31
BON stratigraphic section	41	31
MRD stratigraphic section	71	7
DH stratigraphic section	94	4
New Guinea Point	9	3
Basal sequence, Jackson's Crossing	12	0
Heath's Quarry exclusive of Taravale Fm.	3	0
Cameron's Quarry	6	2
Cameron Member	10	7
Basal sequence, Buchan-Orbost Rd., west of East Buchan bridge	17	0
Boulder Flat	9	5
Tabberabbera	c. 43	3
Top 1m of Buchan Caves Limestone overlooking The Pyramids	6	0

Table 1. Number of samples collected and processed for conodonts, and number of productive samples.
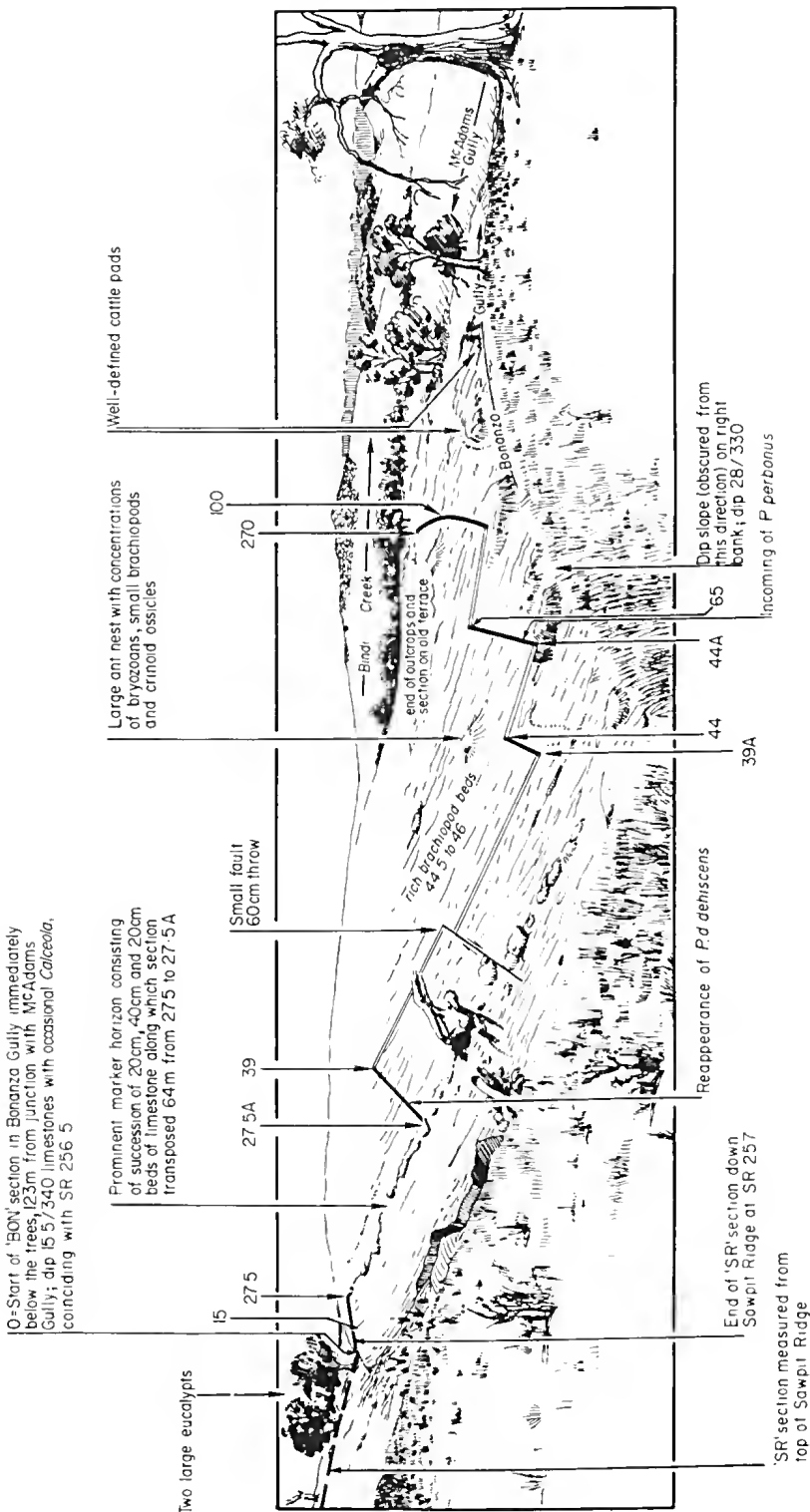
Fig. 6. Panorama (compiled from photographs) of the highly fossiliferous left bank of Bonanza Gully, Bindi, showing position of end of SR section measured down Sawpit Ridge, location of BON section, and positions of offsets along marker horizons. Section BON is located entirely within highly fossiliferous upper Buchan Caves Limestone. Numbers are sample numbers.

solution. The remaining 150 productive samples were generally leached to completion. Illustrations of the conodonts recovered are arranged (Figs. 7–13) according to the sequence of discussion, locality by locality, though with similar forms grouped for comparison.

The overall low productivity and low diversity, apart from the "marginal Polygnathid Biofacies" in the BON section (see below), are interpreted as being connected with the extreme shallowness of most of the environments sampled. The low diversity and high proportion of barren or unhelpful samples has resulted in a measure of imprecision in the conclusions presented below.

As the results obtained concern correlations about the Pragian–Emsian boundary, some comment is appropriate on conodont zonation through the late Pragian and earliest Emsian. In 1989 the International Commission on Stratigraphy ratified the proposal of the Subcommission on Devonian Stratigraphy (SDS) to fix the base of the Emsian at the incoming of *Polygnathus dehiscens*, with the global stratotype being a section in Zinzilban Gorge in the Uzbek Republic. In this section the evolution of *P. pireneae* into *P. dehiscens* has been documented (Yolkin et al. 1989). The *dehiscens* Zone is thus the basal zone of the Emsian, and an interval characterized by the ancestral form *P. pireneae* is thus indicative of latest Pragian.

Conodont faunas from the Road River and Old Camp formations and the Salmontrout Limestone of east-central Alaska enabled Lane & Ormiston (1979) to refine the conodont zonal scheme for the Pragian. They demonstrated the utility of three intervals in the Pragian, a redefined zone of *Eognathodus sulcatus*, an intermediate zone of *E. sulcatus kindlei* (formerly the *E. sulcatus* n. subsp. Zone of Klapper 1977: 41) and, as youngest interval, a zone of *P. pireneae*. The lower boundary of the *pireneae* Zone was defined at the incoming of *P. pireneae*.

Although *P. pireneae* has been identified in faunas from many sequences, e.g. Bathurst Island (McGregor & Uyeno 1972), Spanish central Pyrenees (Boersma 1974), Germany (Al Rawi 1977), Alaska (Lane & Ormiston 1979; Savage et al. 1985) and south-eastern Australia (herein), there are few sections where evolution of *P. pireneae* to *P. dehiscens* and overlapping ranges of the two forms can be demonstrated. The Zinzilban section in Central Asia (Yolkin et al. 1989) is elegant in this regard. The dearth of such sequences seems to be connected with a major regression event, discussed below, during

part of the *pireneae* interval. Our contention that *"Spathognathodus" trilinearis* Cooper should be referred to *Polygnathus* means there are at least two forms of the genus in the late Pragian. More precise understanding of the *pireneae* Zone requires further study of the evolution and precise temporal relationships of the earliest forms of *Polygnathus*.

1. *Cavan Formation (Wee Jasper)*

Conodont data presented in Table 2, although sparse, show *P. pireneae* to occur through a 5.9 m interval from 58.3 to 64.2 m above the base of the CABL section measured at Wee Jasper (Fig. 2C), in samples 69.6 through to 75. In sample 72.5, from 35 m below the base of the strongly outcropping "Cavan Bluff Limestone Member" [62.1 m above the base of the section], *P. dehiscens dehiscens* makes its first appearance. Thus, using the criterion suggested by SDS, we place the Pragian–Emsian boundary provisionally at this level.

The polygnathids and pandorinellinids in the CABL section occur in thinly bedded limestones, the association possibly indicating deeper water than for the various sections of Buchan Caves Limestone sampled for this study. These elements disappeared with the shallowing event indicated by accumulation of the richly coralline (Pedder et al. 1970) "Cavan Bluff Limestone Member"; in this unit the conodont fauna is dominated by ozarkodinans, principally *O. buchanensis* and *O. pseudomiae*. These have no particular stratigraphic importance other than that they arise in the *pireneae* Zone and are common within faunas of *dehiscens* age.

2. *Buchan Caves Limestone*

The Taravale Formation is preserved in only three areas, all synclinal: at The Basin, at Bindi and in the Buchan–Murrindal area. Sections through the Buchan Caves Limestone from the Snowy River Volcanics to the base of the Taravale Formation were accordingly sampled (5–10 kg samples at approximately 1–2 m intervals) in each of these areas (Fig. 2A, B). Outliers of Buchan Caves Limestone occur in the lower reaches of Limestone Creek (Whitelaw 1954, VandenBerg et al. 1981, 1984) in the headwaters of the Indi (= Murray) River. Because the basal sequence of the Buchan Caves Limestone is superbly exposed in Limestone Creek just

Table 2. Distribution of conodont elements in section CABL through the Cavan Formation, Wee Jasper, New South Wales.

Table 3. Distribution of conodont elements in section SL through the Buchan Caves Limestone at The Basin.

Table 2 (section CABL, Cavan Formation)

Metres above base of 'CABL' section	Sample number	Taxon / element	...	TOTALS
		Oulodus murrindalensis Pa		1
		Pb		1
		M		2
		Sa		3
		Sb		4
		Sc		1
		Polygnathus d. dehiscens Pa		3
		P. d. abyssus Pa		6
		P. pireneae Pa		6
		Ozarkodina buchanensis Pa		43
		O. linearis Pa		3
		O. prolata Pa		4
		O. pseudornae Pa		42
		O. selli Pa		1
		O. sp. A Pa		6
		Pandorinellina e. philipi Pa		3
		Coelodontus sp.		4
		Drepanodus sp.		40
		Non-platform elements Pb		17
		M		4
		Sa		18
		Sb		28
		Sc		

Table 3 (section SL, Buchan Caves Limestone)

Metres above base of 'SL' section	Sample number	Taxon / element	...	TOTALS
		Oulodus murrindalensis Pb		1
		Sa		3
		Sc		134
		Ozarkodina buchanensis Pa		6
		O. linearis Pa		9
		O. prolata Pa		1
		O. sp. A Pa		36
		O. pseudornae Pa		1
		O. sp. indet Pa		2
		Panderodus unicostatus M		35
		Pb		5
		Non-platform elements M		2
		Sa		9
		Sb		21
		Sc		

upstream from Dead Horse Creek, a section was closely sampled commencing in the bed of Limestone Creek (Fig. 3A).

Though the SL section through the Buchan Caves Limestone at The Basin (Fig. 2A) yielded no polygnathids (Table 3), this may be connected with excessively shallow water and have no age significance. *O. buchanensis, O. linearis* and *O. pseudomiae* first appear at 22.5 m, 31.5 m and 39 m respectively above the base of SL. All three species are present at the same stratigraphic level as the first polygnathids, for example in the CABL section at Wee Jasper, but there are no constraining data regarding their first appearances. At 46.5 m, *O. prolata*, not known to occur in horizons of pre-dehiscens age (Mawson 1987a; Bultynck 1989), makes its first appearance; this is consistent with a *dehiscens* age for at least the upper third of the section. The persistently high dolomitic component and thinness of the Buchan Caves Limestone at The Basin relative to sequences elsewhere in the Buchan–Bindi–Snowy River area is taken to be consistent with a topographic high, on the surface of which the Buchan Caves Limestone accumulated.

In the combined SR–BON section measured at Bindi (Fig. 5; Tables 4, 5), *P. dehiscens dehiscens* occurs in a short interval commencing at 64.6 m above the base of the section, and *O. prolata* first appears a further 42.8 m up section. Again, *O. buchanensis* is present from the base of the section, with *O. pseudomiae* appearing only a few metres before *P. d. dehiscens*. The incoming of *P. perbonus* and *P. nothoperbonus* at BON 46–50, 129.6 m above the base of the section, heralds the start of the *perbonus* Zone. In the combined SR–BON section, the transition of *Pand. exigua philipi* to *Pand. exigua exigua* can be traced from true *Pand. exigua philipi* 98.8m above the base of the section, through a transitional form at 107.9 m, to *Pand. exigua exigua* from 110.6 m upwards. Worthy of note is the upper limit of *O. pseudomiae*, 7 m into the *perbonus* Zone, and the loss of *O. buchanensis* just 3.5 m below beds indubitably referrable to the *perbonus* Zone.

The MRD section at East Buchan (Fig. 5; Table 6) was disappointing; only 7 of the 71 samples yielded conodonts. However, the presence of *P. d. dehiscens* 82.5 m above the base of the section indicates *dehiscens* Zone for at least some of the section. Section DH (Table 6), near the junction of Dead Horse Creek with Limestone Creek, yielded elements of *O. linearis* consistent with a *dehiscens* age (Mawson 1987a).

A basal sequence of Buchan Caves Limestone was sampled in the road cutting on the Buchan–Orbost road immediately west of the East Buchan bridge where there are excellent exposures of carbonates interbedded with clastics derived from a volcanic terrane (Talent 1989); all samples proved barren. Another barren basal sequence is well exposed at Jackson Crossing on the left (north) bank of the Snowy River just downstream from the ford; in this area, the Buchan Caves Limestone rests unconformably on Snowy River Volcanics.

O. buchanensis, O. pseudomiae and *Oulodus murrindalensis* were obtained from samples of the "Cameron Member" of the Buchan Caves Limestone 1.2 km east of the Back Creek bridge, East Buchan. Associated with the fauna is a new species of the dacryoconarid *Volynites* apparently derived from *V. velaini* (Munier-Chalmas) and thought (G. K. B. Alberti, pers. comm.) to be consistent with a *pirenae* age or younger. Samples from New Guinea Point (Fig. 1; Table 6) were taken through the middle of the Buchan Caves Limestone outcropping on the New Guinea Point jeep track approximately 1.8 km up the track from the helipad. Spot samples from seemingly low in the Buchan Caves Limestone in the Butchers Ridge and Round Mountain outliers proved unproductive, as did samples from the uppermost part of the Buchan Caves Limestone on "Davidson's Ridge" at Jacksons Crossing.

Because of lack of adjacent outcrop, the limestones in the vicinity of Martin Cameron's Quarry, 6.7 km south-south-west of Buchan, were once thought (Teichert & Talent 1958: 18) to be possibly a carbonate buildup within the Taravale Formation, but closer investigation (Fletcher 1963) showed them to belong to the Buchan Caves Limestone. The limestones at Martin Cameron's Quarry are richly fossiliferous, with stromatoporoids (Ripper 1937), rugose corals and especially tabulate corals dominating the fauna. Despite processing large quantities of limestone relatively free of corals and stromatoporoids, the only conodonts obtained were *O. buchanensis, O. linearis, O. pseudomiae* and *Oulodus murrindalensis*. Of these, *O. linearis* is not known for certain from pre-*dehiscens* horizons.

Limestones in the vicinity of Heath's Quarry in the headwaters of Tara Creek, 6.5 km south of Buchan, have also been construed as part of a carbonate buildup (Teichert & Talent 1958: 16; Talent 1988: 322), but developed within the upper Buchan Caves Limestone. The Heath's

Metres above base of 'SR' section		2.2	10.8	14.6	18.3	54.2	54.9	55.0	57	58.4	58.9	61.9	64.6	65.5	66	79.9	87.3	88.3	89.3	93.2	98.2	98.8	101.7	106.3	106.8	107.4	107.9	108.8	110.6	111	113.2	114.7	114.9	TOTALS
Sample number		6	29	39	45	100/1	102	104	106.8	109.5	110.5	117.5	125	127.5	129	166	185	187.5	190	200	213	214.5	222	234	235.5	237	238	240.5	245	247	252.5	256.5	257	
Oulodus murrindalensis	Pa														1	1																		2
	Pb						1																											1
	M						1																											1
	Sa														3																			3
	Sb															1																		1
	Sc							1							1	4																		7
Polygnathus d. dehiscens	Pa												10	1																				11
Ozarkodina buchanensis	Pa	1		1		13	6	1	5	3			2		63	5	39				1	6	2	1		1	1		44	22	1	2	5	225
O. e. excavata	Pa																	1																1
O. linearis	Pa														4		3	2	6		1	1	3		1	1	1	1	11	11	1		1	48
O. prolata	Pa																	1									2	2	49	18	5	5		82
O. pseudoornae	Pa					2		1		1					10												1							15
Pandorinellina e. exigua	Pa																												19	9	2	4	13	47
Pand. e. philipi	Pa														7		1		4	5	1													18
Transitional to P. e. exigua	Pa																										1		6	6				13
Panderodus unicostatus	M														15		8		1	3	2	2	1		1			1	220	22	3		6	285
Non-platform elements	Pb			1		3			1	1	1				9	2	12		1	1	2	2	2						2		12	12	2	66
	M					3				1							2													4	2	1	1	14
	Sa							1							1		5	1	1				1		1						2	1	1	14
	Sb						1	1							1		3	1	1						2						2			12
	Sc		1			1	2		2						1	10	3	4	1	3	4										15	12	2	61

Table 4. Distribution of conodont elements in section SR through the Buchan Caves Limestone along Sawpit Ridge, Bindi.

Metres above base of 'BON' section		114.7	119 - 119.5	119.5 - 120.9	121.5 - 122	122.6 - 123.4	123.9 - 125	126.1 - 127	129.6 - 131.5	131.5 - 132.5	132.5 - 136.4	136.4 - 138.6	138.6 - 140.9	155 - 159.7	180.8 - 183.6	184.6 - 187.9	188.3 - 192.6	195.8 - 204.3	204.7	211.3 - 220.7	220.7 - 234.8	TOTALS
Sample number		0	13.5 - 15	15 - 19.5	21 - 23	25 - 27.5	29 - 35	36 - 39	46 - 50	50 - 56	56 - 60.5	60.5 - 65	65 - 70	100 - 110	155 - 161	163 - 170	171 - 181	187 - 205	206	220 - 240	240 - 270	
Oulodus murrindalensis	Pa								1													1
	M					2			2													4
	Sb					1																1
	Sc					1			2	1			1	1								6
Polygnathus dehiscens dehiscens	Pa						1	6	3													10
Transitional to P. nothoperbonus	Pa							4	4												1	9
P. nothoperbonus	Pa								7	1	2	3									2	15
P. dehiscens abyssus	Pa						1	6	9		1	1										18
Transitional to P. perbonus	Pa								1		1											2
P. perbonus	Pa								2		3	1						1				7
Ozarkodina buchanensis	Pa		12						2													14
O. excavata excavata	Pa								1													1
O. linearis	Pa		2			5		1	3	1			1			1						14
O. prolata	Pa		6	8	16	7	35	47	29	18	18	39	21				2					246
O. pseudoornae	Pa		2					2				2										6
Pandorinellina exigua exigua	Pa	6	49	13	15	9	28	9	9	4	7	1	4			1	6	1	3	7	6	178
Belodella devonica					1							1										2
Panderodus unicostatus	M		7																			7
	S	1	28		2	3	2	4	1	1	2	4	1			2				2	1	54
Non-platform elements	Pb		1	4		2	18	18	12	3	7	11	3			3		1		2	2	87
	M		2			1	1	6	2	3	1						1			1		18
	Sa			1	1	2	1															5
	Sb							1														1
	Sc		58	4	5	7	8	7	18	3	1	3	2			4		1		1	2	124

Table 5. Distribution of conodont elements in section BON through the upper Buchan Caves Limestone commencing at SR256.5 in Bonanza Gully, Bindi.

Quarry limestone body is most unlike the Buchan Caves Limestone elsewhere in eastern Victoria. It is light grey and extraordinarily fossiliferous with a great diversity of stromatoporoids (Ripper 1937), algae and massive, fasciculate and ramose tabulate corals as well as occasional cerioid and phaceloid rugose corals (Hill 1950).

No conodonts were obtained from the massive limestones exposed in the quarry and its immediate vicinity, but limestone nodules from the Taravale Formation outcropping intermittently in the gutter along the access road leading southwards from the quarry produced polygnathids transitional from *P. dehiscens* to *P. perbonus*. A sample 20 m along the gutter from the southernmost outcrop of limestone at the quarry, equivalent to just a few metres stratigraphically (outcrops are poor) above the Buchan Caves Limestone, produced five such specimens. Four specimens of the same transitional form were found previously, about 0.8 km to the north in outcrops along the old track to the site of McRae's former Taravale Homestead, 3 m stratigraphically above the Buchan Caves Limestone (Mawson 1987a, Tables 2 and 5, sample OTRC 5).

If comparison is made with the conodont faunas from samples collected from the entrance cutting to the Buchan Caves Reserve 6.5 km away, the horizon with polygnathids transitional from *P. dehiscens* to *P. perbonus* in the vicinity of Heath's Quarry equates approximately with sample BCE 3 (Mawson 1987a, Table 3), 61.8 m above the base of section BCE. This is equivalent to approximately 114 m above the top of the Buchan Caves Limestone.

If we assume the transitional forms *P. dehiscens* to *P. perbonus* in the vicinity of Heath's Quarry and in the vicinity of the Buchan Caves Reserve occur at approximately the same stratigraphic level, the contrast in stratigraphic position (c. 3 m versus c. 114 m) relative to the top of the Buchan Caves Limestone is far greater than would be anticipated over such a short distance (6.5 km). This is surprising given the relative uniformity in stratigraphy of the Buchan Caves Limestone over so much of the Buchan–Murrindal–Gillingall–Jacksons Crossing area (Talent 1956, 1969). We infer from this that the Heath's Quarry buildup may have had appreciable relief and grown entirely (or perhaps continued growing) long after the transgressive event expressed by the spreading of the Taravale Formation (and the onset of pelagic conditions) over most of the area.

3. *Loyola*

Our sampling in quest of additional data on the occurrences of early polygnathids at Loyola proved unsuccessful, but identifications of other forms we obtained are noted (Table 6). *Polygnathus trilinearis* (Cooper) occurs at the Kiln Quarry whereas *P.* cf. *pireneae* has been found only at Griffiths' Quarry. That such forms may occur in association must rest on evidence from not very well preserved material documented here from Boulder Flat. Better preserved material of *P. trilinearis* occurring in association with indubitable *P. pireneae* has been obtained from a clast in the lower Cunningham Formation 6.2 km north-north-west of Mumbil in west-central New South Wales (Talent & Mawson in prep.)

4. *Boulder Flat*

Five localities we sampled proved productive (Table 6). One of these, locality 5, corresponds to VandenBerg's (in Pickett 1984) productive locality C811; his other productive locality, C810, seems to correspond to our locality 4. All produced polygnathids: four with *Polygnathus trilinearis* (Cooper), three with *P.* cf. *pireneae* Boersma, two of these with both forms associated. Our sampling thus failed to produce evidence of horizons older or younger than the latest Pragian *trilinearis–pireneae* interval, probably not older than the lower part of the Buchan Caves Limestone. Our sampling demonstrates that *Amydrotaxis* (Fig. 9M) can occur in association with *Polygnathus pireneae*; the genus *Amydrotaxis* thus persisted into latest Pragian times.

We were unable to confirm Pickett's (1984) report of *Delotaxis* (= *Oulodus*) *tenuistriata* from Boulder Flat, but indubitable *O. tenuistriata* occurs in association with *P. pireneae* in limestones of the "Coopers Creek Formation" outcropping on the left side of the Tyers River beneath the bridge at grid reference 494805 on 1:25,000 topographic map 8121-1-1 Rintoul Creek. *O. tenuistriata* thus extends from at least the *eurekaensis* Zone (Mawson 1986) through into at least the *pireneae* Zone.

Additionally, data from the Black Watch Member of the Bungywarr Formation (see earlier) at Boulder Flat indicates that the stratigraphically important brachiopod genus *Spinella* extends downwards to at least the *pireneae* Zone.

Evidence to hand is thus consistent with the limestones at Boulder Flat aligning in a general

LOCALITY	Element	McColl's Dam	127 (63)	140 (68.7)	165 (82.5)	178 (89)	223 (111.5)	312.5 (152.2)	445 (222.5)	DEAD HORSE CK.	NGP 3	NGP 5	NGP 6	TAB 97	TAB 92	TAB 52	BF 3	BF 4	BF 6	BF 7	BF 5	Kiln Q.	Griffith's Q.
Pelekysgnathus sp.	Pa												1								1		
Oulodus murrindalensis	Pb																	3					
	M					1																	
	Sa		1			1					1												
	Sb																	1					
	Sc																	2					
Oulodus sp.	Pa											1		1									
Polygnathus d. dehiscens	Pa				1																		
P. cf. pireneae	Pa																1	3		1			
P. trilinearis	Pa													1				2	1	3	4	[1]	
Polygnathus sp.	Pa																						[2]
Ozarkodina buchanensis	Pa	3					2		3			1					1	1			1	[3]	[3]
O. excavata	Pa	3																					
O. linearis	Pb															1							
	Sa									1													
	Sb									1													
O. cf. optima	Pa														1								
O. prolata	Pa								9														
O. pseudomiae	Pa	2		1			4		1					cf1								3	2
Ozarkodina sp.	Pa																				1		
Pandorinellina ex. philipi	Pa													1			1		1	7	15		
Pand. s. steinhornensis	Pa													1									
Amydrotaxis sp.	Pa																			1	?1		
	Pb																		1		1		
	Sc																				1		
Belodella devonica																						2	
Belodella resima																1						1 [1]	
Drepanodus sp.																1		1				[1]	
Neopanderodus aequabilis																1				1	1		
Panderodus unicostatus																					2		
Panderodus cf. valgus																1							1
Non-platform elements	Pb	2					1	1	2					3		1	1				1	[1]	1
	M								2							1							
	Sa																					[3]	
	Sb	3					1		1										1		2	1	
	Sc	3					1		4			1									2	1 [1]	

Table 6. Distribution of conodont elements in section MRD through the Buchan Caves Limestone at East Buchan, New Guinea Point, in the DH section at the junction of Dead Horse and Limestone creeks, and at Tabberabbera, Boulder Flat and Loyola. Identifications based on Cooper (1973) are shown "boxed".

way with the Buchan Caves Limestone, the underlying sedimentary–volcanic sequence ("Bungywarr Formation") equating with an unspecified portion of the upper Snowy River Volcanics. The principal difference between the sequences in the two areas is that the "Bungywarr Formation" is more marine and less volcanic than typical Snowy River Volcanics sequences to the west. We accordingly follow Thomas (1949) in regarding the fault-preserved sedimentary–volcanic sequence at Boulder Flat ("Errinundra Group") as being best viewed as an outlier of the Snowy River Volcanics–Buchan Group succession rather than being the preserved record of a discrete "small rift-like extensional basin" with carbonate sedimentation commencing significantly earlier than at Buchan, for example.

5. *Waratah Bay*

Though not unexpected from an horizon such as the Bell Point Limestone, we do not accept the identification of the pivotal form *Polygnathus pireneae* Boersma in Argent's sample 163 from the mashed occurrence of *Amphipora*-rich limestones of this unit at The Bluff (= Bluff Member of Teichert 1954). The illustrated specimen (Bischoff & Argent 1990, pl. 3, fig. 14) lacks the medial row of denticles essential for reference to *Polygnathus*. We interpret it as a specimen of *Eognathodus sulcatus* with an oblique crack. Available conodont data thus does not provide precision regarding correlation of the Bell Point Limestone, nor a clear indication as to the time represented by the unconformity between the Waratah and Bell Point limestones.

Contra Bischoff & Argent (1990), we feel there is no compelling evidence from which to infer an interval referrable to the *pesavis* Zone in the lower part of the Waratah Limestone at Walkerville and Grinder Point. We attach little significance to absences, in this instance of *Eognathodus sulcatus* morphs, especially as the earliest morphs transitional from *Ozarkodina pandora* are not present. There are thus, in our view, no grounds for considering the transgression represented by the basal Waratah Limestone to have predated the limestones of the Tyers–Boola area from which *E. sulcatus* was first described (Philip 1965). They may well have been coeval, as was postulated elsewhere (Talent 1965, 1967, 1989; Talent & Yolkin 1987).

6. *Tabberabbera*

The Wentworth Group includes at least 25 significant limestone lenses, though most carbonate developments are conspicuously lacking or poor in macro-fossils. In the hope of obtaining greater precision in alignment of the Wentworth Group with the conodont zonal scheme presently accepted for the Early Devonian, most carbonate horizons delineated in earlier mapping (Talent 1963) were sampled, most by 5–10 kg samples, some more copiously. Because the Tabberabbera area and the Tabberabberan Orogeny have such prominence in the geology of eastern Australia, the results of this investigation, though largely negative, are presented here.

Only three horizons proved fruitful: limestone boulders in the Wildhorse Formation at locality 97 (Scenic Lookout), and autochthonous limestone lenses in the Kilgower Member of the Tabberabbera Formation at localities 52 and 92 (Fig. 3A; Table 6). The largest limestone lens in the Kilgower Member, extending across the Rocks Creek–Pat Creek divide, was extensively sampled in the vicinity of locality 51 and where it outcrops in road cuttings on the new road from Cobbannah Creek to Angusvale; all samples proved to be barren of conodonts. Limestone cobbles in the Wild Horse Formation at locality 97 occur over a distance of c. 95 m along the road cutting, are exceptionally up to 50 cm in size, and are often coarsely crinoidal, dolomitic and pyritic. We know of no potential source for these limestones. As they were already lithified before incorporation into the Wild Horse Formation, an appreciable age-difference between them and the Wentworth Group is conceivable. We believe, however, that any age-difference is most likely trivial—much less than can be discriminated on the basis of presently known ranges of late Pragian conodonts.

We infer from our data from Boulder Flat, where *Polygnathus trilinearis* occurs in association with *P.* cf. *pireneae*, that the occurrence of *P. trilinearis* in limestone clasts in the Wild Horse Formation is best interpreted as evidence for an age not appreciably older than the *pireneae* interval. The other forms obtained, *Pand. steinhornensis steinhornensis, Pand. exigua philipi,* and *O. pseudomiae*, are consistent with this age assignment. A measure of caution should be exercised, however, as we do not have high quality data globally for the time-ranges of these forms and, moreover, we need more precise data regarding evolution of the earliest polygnathids *P. pireneae* and *P. trilinearis* in the late Pragian. The age indicated is thus very close to that previously advocated for the Wild Horse Formation and Kilgower Member (Talent 1963).
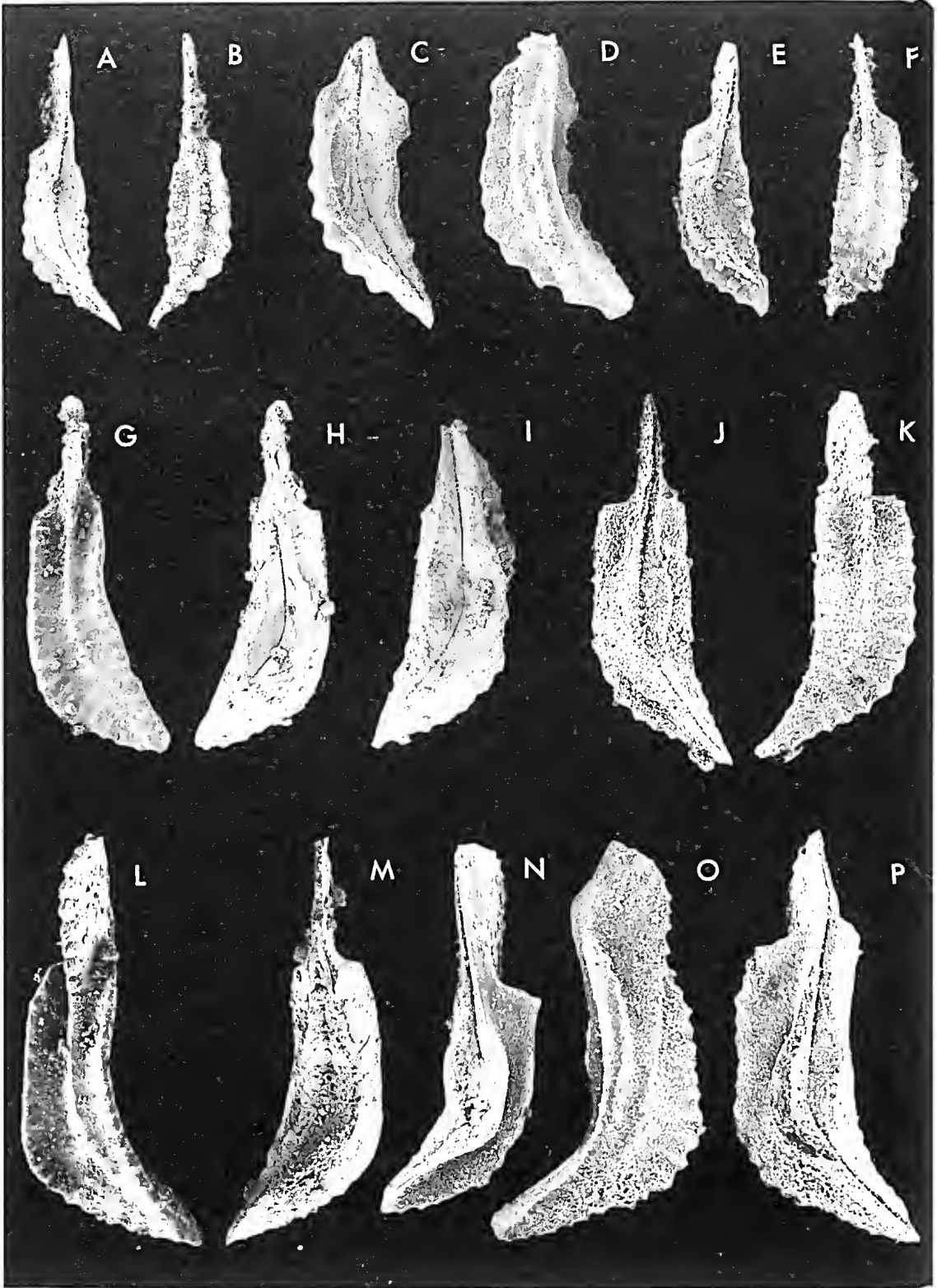
Limestone lenses in the Roaring Mag Member of the Tabberabbera Formation were sampled extensively at Whitbournes Point in Sandys Creek, on the Gorge Gully–Sandys Creek divide, and at Horseshoe Bend, Tabberabbera; all, surprisingly, proved barren. These limestones are thin, interbedded with siltstone, generally 1–3 cm in thickness, often stylolitic or intricately sheared, and are notable for rarity or lack of macrofossils. The limestone lenses and associated clastics in the vicinity of the Horseshoe Bend saddle contain deformed brachiopods tentatively assigned to *Spinella* and *Buchanathyris*. It was on the basis of these that the Roaring Mag Member was suggested to be broadly correlative with the Buchan Caves Limestone (Talent 1963). Silicified gastropods, worms (cf. *Spirorbis*) and occasional brachiopods (including ?*Spinella and Buchanathyris*) were obtained from the prominent limestone outcropping immediately north of the junction of Sandys Creek with the Mitchell River (illustrated by Easton 1938). This unit proved to be barren of conodonts.

We can therefore add no new data that may help arrive at a more precise age for the Roaring Mag Member. However, conodont data presented here for the Wild Horse Formation and Kilgower Member suggest that the transgression represented by the basal units of the Wentworth Group probably aligns with the transgression represented by the Buchan Caves Limestone and not with the transgression represented, for instance, by the Waratah Limestone at Waratah Bay (Talent 1989). If this is accepted, the transgression inferred to have been connected with the deepening represented by the Roaring Mag Member may align with the deepening event expressed by the swift change from shallow shelf Buchan Caves Limestone to pelagic Taravale Formation at Buchan and the deepening within the upper Buchan Caves Limestone at Bindi, i.e. commencing late in the *dehiscens* Zone.

7. Conclusions

Despite low diversities, low yields and a high proportion of barren samples, conodont data indicate approximate contemporaneity of the Buchan Caves Limestone, the Cavan Formation, the limestone at Boulder Flat, the presumed olistostromal limestones at Loyola, the uppermost carbonate horizons of the "Coopers Creek Formation" at Tyers (Mawson et al., in prep.) and, seemingly, the lower part of the Wentworth Group and perhaps the Bell Point Limestone at Waratah Bay. All, with the exception of the last, have produced conodonts indicative of the latest Pragian *pireneae* Zone (or Subzone). The Pragian–Emsian boundary clearly lies within the Cavan Formation below the "Cavan Bluff Limestone" and within the Buchan Caves Limestone. High precision eludes us, however, regarding correlation of the lowest horizons of the Cavan Formation (due to absence of carbonates), the Buchan Caves Limestone (due to dolomites), and the limestone at Boulder Flat (bad outcrops and barrenness). All conceivably could extend from the *pireneae* interval down into the *kindlei* interval *sensu stricto* but, in the absence of any hint of this in the conodont data presently available to us, and in view of general considerations discussed below, we do not view this as probable.

It seems clear, nevertheless, that all of the above coeval or approximately coeval units, the Roaring Mag Member apart, reflect aspects of a transgressive event that was widespread in south-eastern Australia. It had been assumed earlier (Talent & Yolkin 1987; Talent 1989) on the basis of data then available that this event probably aligned with the base of the *dehiscens* Zone, the base of cycle Ib of Johnson et al. (1985). They had suggested a global transgression event near the base of the *dehiscens* Zone (in fact, just prior to it in Central Asia), an earlier transgressive event commencing at about the *sulcatus–kindlei* boundary, and an intervening major regressive phase aligning approximately with the *pireneae* interval. Unpublished data (Mawson & Talent 1992; Talent & Mawson, in prep.) from the Wellington–Mumbil–Stuart Town area of east-central New

---

Fig. 7. A–F, *Polygnathus pireneae* Boersma. A, B, NMV P142080, Pa element lower and upper views, × 70, CABL67.6. C, NMV P142081, Pa element lower view, × 100, CABL71. D, NMV P142082, Pa element upper view, × 60, CABL73.4. E, F, NMV P142083, Pa element lower and upper views, × 50, CABL75. G, H, *Polygnathus pireneae–dehiscens* transitional form, NMV P142084, Pa element upper and lower views, × 45, CABL76. I–K, *Polygnathus dehiscens dehiscens* Philip & Jackson. I, NMV P142085, Pa element lower view, × 60, SR125. J, K, NMV P142086, Pa element lower and upper views, × 60, BON46–50. L–N, *Polygnathus dehiscens abyssus* Mawson. L, M, NMV P142087, Pa element upper and lower views, × 60, SR125. N, NMV P142088, Pa element lower view, × 60, SL80. O, P, *Polygnathus nothoperbonus* Mawson, NMV P142089, Pa element upper and lower views, × 60, BON46–50.
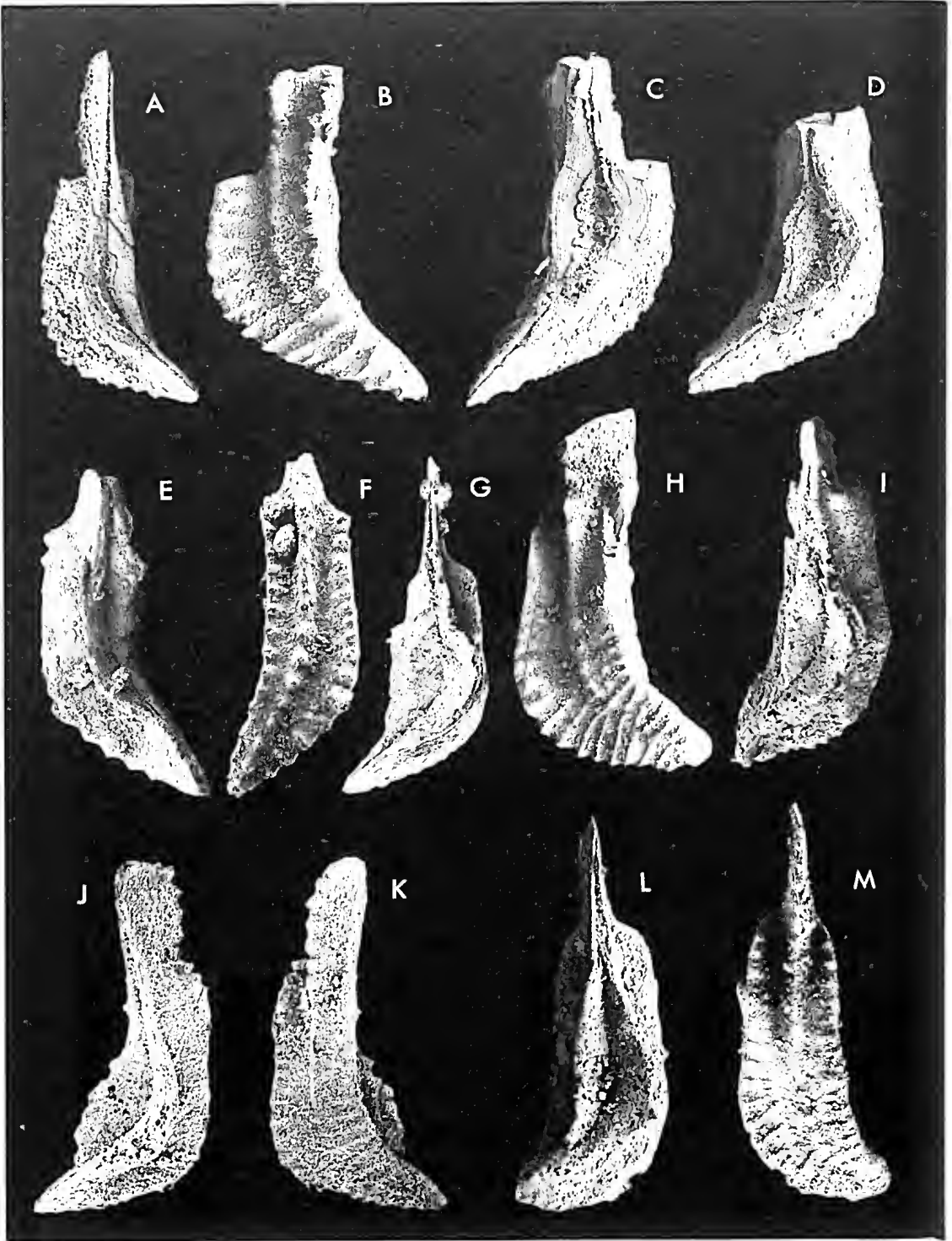
South Wales are in accord with a regressive event with platform exposure and development of submarine fans (Red Hill "Limestone") having occurred *within* and seemingly having been terminated by major transgression *before* the end of the *pireneae* interval. If the data from the Wellington–Mumbil–Stuart Town area and from south-eastern Australia reflect global eustatic events rather than local tectonic events, and if the transgressions and regressions in the two areas were coeval, the major transgressions represented by the Buchan Caves Limestone and Cavan Formation may have occurred within the *pireneae* interval, presumably very early in it, rather than aligning with the Johnson et al. (1985) transgression at about the *sulcatus–kindlei* boundary. Unfortunately, data presently to hand are not sufficient for an unequivocal answer to this question.

INFERRED CONODONT BIOFACIES

It has been pointed out elsewhere (Mawson et al. 1988; Mawson & Talent 1989) that, during Early Devonian times in eastern Australia, near-shore environments were populated principally by conodont animals bearing ozarkodinan elements or simple cones, whereas elsewhere icriodids were typical of this environment. Symptomatic of this virtual exclusion is that, despite much conodont work on the Lower Devonian of Victoria, only one icriodid has been reported to date, namely from the lower Pragian at Tyers (Philip 1965). It is not uncommon for Australian Early Devonian faunas to be dominated by ozarkodinans and simple cones to the virtual exclusion of all other forms; for example, in the SL section at The Basin (Table 3). For Australia, therefore, an Ozarkodinan Biofacies was substituted for the Icriodid Biofacies of the northern hemisphere. Clearly, for reasons unknown, such icriodid lineages as reached Australia during the Devonian were unable to proliferate, despite an abundance of near-shore environments that one might imagine to have

been appropriate. These, admittedly, were subject to major transgressive and regressive (T/R) events destabilizing the environment (Talent & Yolkin 1987; Talent 1989), some of these events having been connected with regional orogenesis. But T/R events, even if not always as spectacular as those experienced in eastern Australia, occurred globally during the Early Devonian (Johnson et al. 1985).

In somewhat deeper, relatively quieter waters than those typical of the Ozarkodinan Biofacies, polygnathids and pandorinellinids were generally dominant, forming a Polygnathid Biofacies. Such, for example, is typical of the nodular limestones, shales and impure limestones of the Emsian (late *dehiscens* to *serotinus* zones) Taravale Formation at Buchan, Bindi and The Basin (Mawson 1987a; Mawson et al. 1988). The incoming of this biofacies coincides with the incoming of pelagic elements, specifically ammonoids and dacryoconarids, and significant change in the brachiopod and coral faunas (Talent 1985). Tabulate corals, stromatoporoids, algae and sponges virtually disappear. This event, within the *dehiscens* Zone, has been interpreted as an especially widespread, possibly global transgression (Talent & Yolkin 1987; Talent 1989). The change from Ozarkodinan to Polygnathid biofacies is apparent in the combined SR–BON section at Bindi and the CABL section at Wee Jasper.

The Basin

The SL section at The Basin (Fig. 2A, Table 3) is unequivocally representative of the Ozarkodinan Biofacies; all Pa elements of the fauna are ozarkodinans. The remarkably low diversity in brachiopods, restricted to *Spinella* and *Buchanathyris* to the virtual exclusion of all others, occasional tabulate corals, mainly species of *Favosites* and *Syringopora*, and of rugose corals, principally *Chalcidophyllum recessum* (Hill) and very rare *Acanthophyllum*, is consistent with very shallow water, possibly of abnormal salinity. An interval with high diversity in silicified

---

←

Fig. 8. A, *Polygnathus dehiscens dehiscens–nothoperbonus* transitional form, NMV P142090, Pa element lower view, × 75, BON36–39. B–D, *Polygnathus nothoperbonus* Mawson. B, C, NMV P142091, Pa element upper and lower views, × 60, BON60.5–65. D, NMV P142092, Pa element lower view, × 60, BON60.5–65. E–K, *Polygnathus perbonus* (Philip). E, F, NMV P142093, Pa element lower and upper views, × 80, SR125. G, NMV P142094, Pa element lower view, × 45, SL60. H, I, NMV P142095, Pa element upper and lower views, × 45, BON56–60.5. J, K, NMV P142096, Pa element lower and upper views, × 60, BON46–50. L, M, *Polygnathus dehiscens abyssus–perbonus* transitional form, NMV P142097, Pa element lower and upper views, × 60, BON36–39.
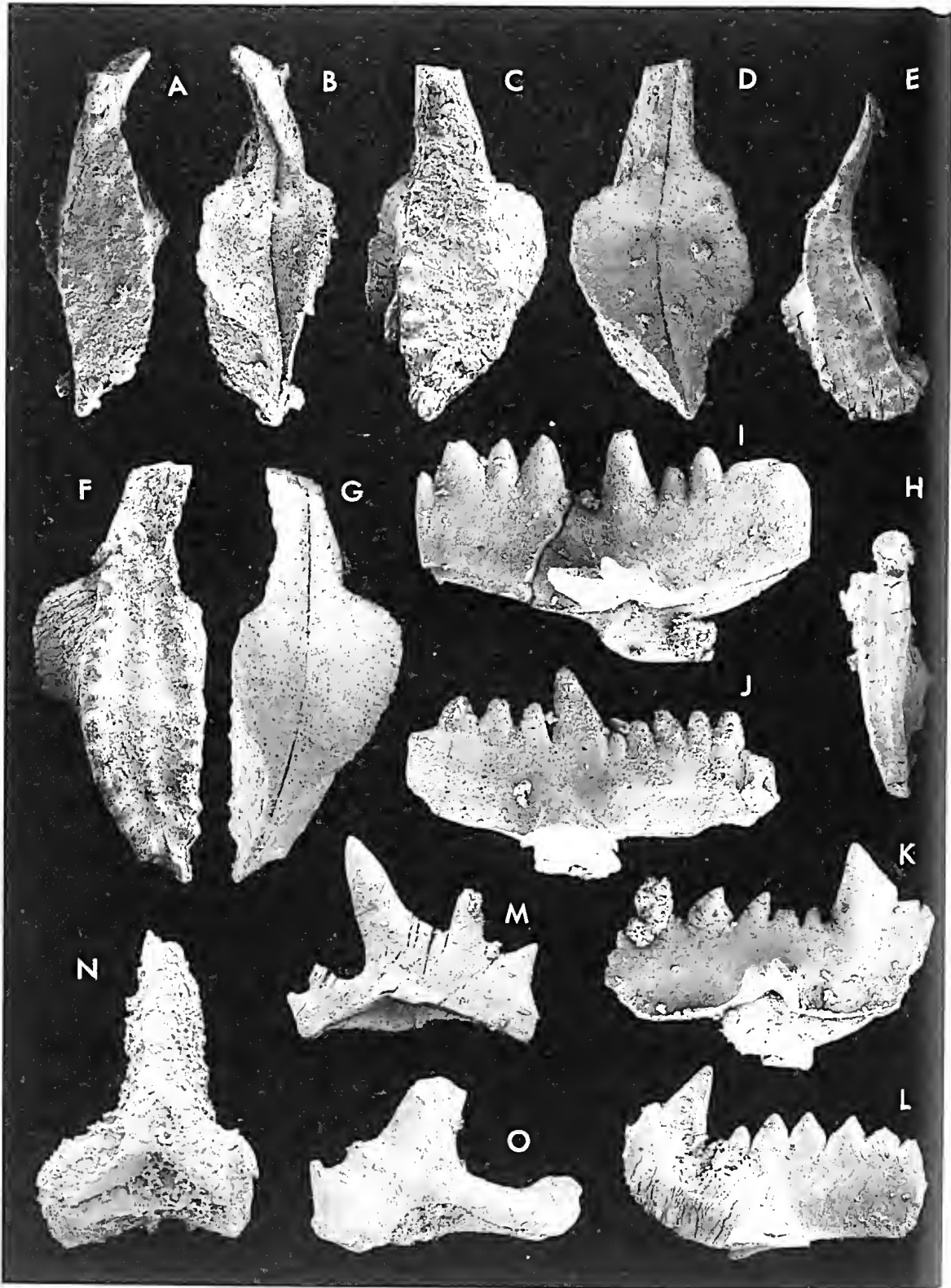
Phase	Metres above base of composite section	Ratio $Oz + S : Pa + Po$	Salient features of fauna	Inferred relative depth
1	0 - 61.9	34 : 1	No polygnathids	Very shallow
2	64.6 - 65.5	1 : 6	Brief incoming of polygnathids	Brief deepening event
3	66 - 108.8	15 : 1	Pandorinellinids persist but no polygnathids present	Shallow conditions, but not as shallow as in Phase 1
4	110.6 - 123.4	3 : 1	Prevalence of pandorinellinids	Deepening
5	123.9 - 234.8	1 : 1.17	Reappearance and persistence of polygnathids	Further deepening; marginal Polygnathid Biofacies

Table 7. Ratios of conodont genera, and inferred relative water depths of faunas from the combined SR–BON section at Bindi. Oz = ozarkodinans, S = simple cones, Pa = pandorinellinids, and Po = polygnathids.

molluscs, principally bivalves, occurs near the top of the section, but there is no increase in diversity of brachiopods and apparently no change in lithofacies.

Bindi

The two sections at Bindi, SR (Sawpit Ridge) and BON (Bonanza Gully), taken together, provide a continuous section through the Buchan Caves Limestone (BON 0 is the projection northwards along strike of SR256.5; Tables 2 and 3; Fig. 6). A succession of five conodont biofacies can be discriminated (Table 7). The first 61 m of section, Phase 1, is dominated by ozarkodinans; in Phase 2, between 66.6 and 65.5 m, there is a brief deepening event with incoming of a few polygnathids. During Phase 3 shallow conditions resumed but in Phase 4, commencing at 110.6 m above the base of the section, the fauna was enhanced by entry of relatively abundant pandorinellinids, otherwise typical of the Polygnathid Biofacies but not in sufficient numbers for the interval to be referred to that biofacies.

During Phase 5, commencing 123.9 m above the base of the composite section, polygnathids appeared again and persisted, marginally outweighing ozarkodinans and simple cones. This last phase is therefore referred to as a marginal Polygnathid Biofacies.

In a paper on lower Middle Devonian conodonts from north-central Ohio, Sparling (1984) included species of *Panderodus* together with polygnathids when establishing biofacies units; he assigned other simple cones to shallower biofacies. If Sparling's lead were to be followed for the SR–BON section, both Phase 4 and Phase 5 would have an ozarkodinan + simple cone − *Panderodus versus* polygnathid + pandorinellinid + *Panderodus* ratios of close to 1:2. Both could therefore be referred to the Polygnathid Biofacies.

East Buchan

The MRD section at East Buchan yielded very poorly, doubtless because of excessively shallow water. Dolomite is more abundant in this

←

Fig. 9. A–G, *Polygnathus trilinearis* (Cooper). A, B, NMV P142098, Pa element upper and lower views, × 60, BF3. C, D, NMV P142099, Pa element upper and lower views, × 80, BF7. E, NMV P142100, Pa element upper view—note the centre row of denticles forming the blade, × 45, BF4. F, G, NMV P142101, Pa element upper and lower views, × 40, BF7. H, *Polygnathus* cf. *pireneae* Boersma, NMV P142102, Pa element upper view of broken specimen, × 70, BF4. I, J, *Ozarkodina buchanensis* (Philip). I, NMV P142103, Pa element lateral view, × 60, BF7. J, NMV P142104, Pa element lateral view, × 65, BF7. K, L, *Pandorinellina exigua philipi* (Klapper). K, NMV P142105, Pa element lateral view, × 60, BF7. L, NMV P142106, Pa element lateral view, × 60, BF7. M, *Amydrotaxis* sp., NMV P142107, Pb element lateral view, × 20, BF6. N, O, *Ozarkodina linearis* (Philip). N, NMV P142108, Sa element, × 60, DH49.6. O, NMV P142109, Se element, × 50, DH49.6.
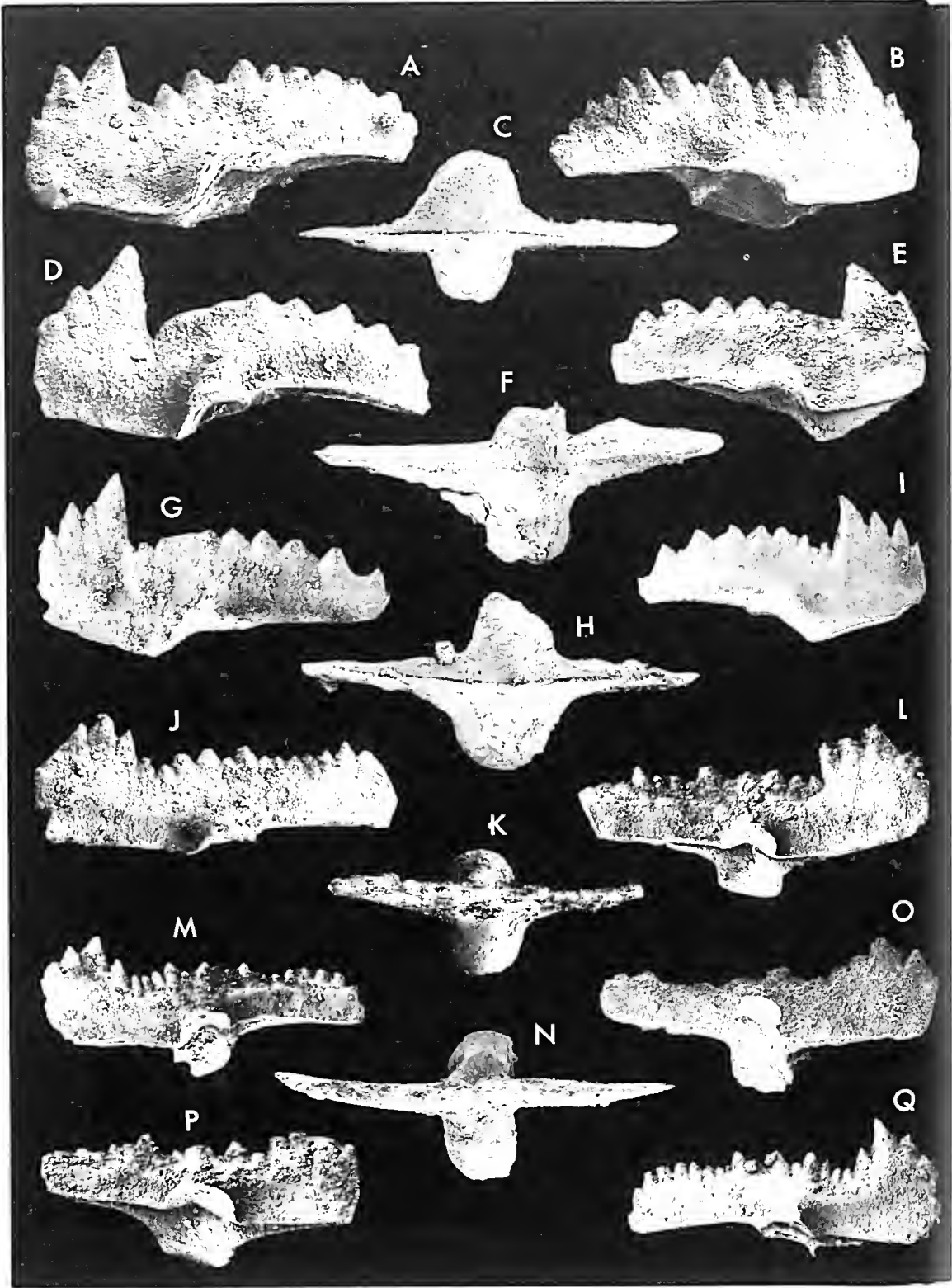
section than in other sections sampled and increases south-eastwards towards the Baek Creek area of East Buchan where it is at a maximum for the Buchan Caves Limestone. No conodonts were recovered from 20 samples collected in the first 126 m of section, though approximately 100 kg from McColl's Dam, a few metres above the base of the Buchan Caves Limestone about a kilometre south of MRD, produced a small fauna. Only 7 of the next 51 samples on the MRD section yielded conodonts. From the little evidence available (Table 5), the MRD section is representative of the Ozarkodinan Biofacies with ozarkodinans outweighing polygnathids 20:1.

Boulder Flat

All productive spot samples from Boulder Flat have polygnathids and pandorinellinids and represent the Polygnathid Biofacies. The ratio of polygnathids plus pandorinellinids to ozarkodinans plus simple cones is 4:1.

SYSTEMATIC PALAEONTOLOGY

As most of the conodont fauna has been fully described in earlier papers (e.g. Philip 1966; Mawson 1987a), we have documented most of the species recovered by means of illustration. Description is limited to forms regarded as new or where comment is deemed necessary. Type and figured specimens are housed in the invertebrate palaeontological collections of the Museum of Victoria (NMV). Precise horizon and locality data for each sample number can be obtained by reference to Figs 1–3 and 5, and Tables 2–6.

Genus **Ozarkodina** Branson & Mehl, 1933

Type species. Ozarkodina typica Branson & Mehl, 1933.

Discussion. Knowledge of the Sa element is pivotal for differentiating *Ozarkodina* from *Pandorinellina.* In *Ozarkodina* the posterior process is expressed as a slight swelling on the posterior base of the cusp ("trichonodellan" form); in *Pandorinellina* this process is well developed ("diplodellan" form) (Klapper & Philip 1971; Klapper in Ziegler 1973). In our collections there is a dearth of Sa elements that can be assigned with certainty to either *Ozarkodina* or *Pandorinellina.* The new species proposed below is referred to *Ozarkodina* rather than to *Pandorinellina* because no diplodellan Sa elements are represented in the collections, and in view of the particular disposition of the anterior denticles along the blade.

Ozarkodina pseudomiae sp. nov.

Fig. 11A–Q

Ozarkodina buchanensis (Philip).—Mawson 1987a, pl. 37, fig. 11 [Pa element].

Etymology. pseudo (Gr. *pseudes* = false), in reference to the superficial similarity to *Ozarkodina miae* Bultynck.

Holotype. NMV P142128 (Fig. 11B) from Buchan Caves Limestone, 40.5m above the base of the SL section (sample SL28) at East Buchan.

Paratype. NMV P142127 (sample SL28) at East Buchan.

Additional material. One hundred and ten specimens from the CABL, SL, SR, and MRD sections, McColl's Dam and Loyola.

Diagnosis. Representative Pa elements of *O. pseudomiae* have a relatively broad, straight blade of medium length with numerous (average 11) small, stubby, triangular denticles. The symmetrical ear-shaped lobes of the basal cavity typically occupy the anterior part of the posterior half of the blade.

Discussion. O. pseudomiae and *Pandorinellina steinhornensis miae* (Bultynck) are easily differentiated on two grounds: the former has fewer,

←

Fig. 10. A–I, *Pandorinellina exigua exigua* (Philip). A, NMV P142110, Pa element lateral view, × 60, SR247. B, NMV P142111, Pa element lateral view, × 60, SR247. C, NMV P142112, Pa element lower view, × 60, SR247. D, NMV P142113, Pa element lateral view, × 45, SR245. E, NMV P142114, Pa element lateral view, × 80, SR256.5. F, NMV P142115, Pa element lower view, × 60, SR256.5. G, NMV P142116, Pa element lateral view, × 60, BON21–23. H, NMV P142117, Pa element lower view, × 60, SR247. I, NMV P142118, Pa element lateral view, × 60, BON46–50. J–Q, *Ozarkodina prolata* Mawson. J, NMV P142119, Pa element lateral view, ×45, SR245. K, NMV P142120, Pa element upper view, × 80, SR257. L, NMV P142121, Pa element lateral view, × 45, SR245. M, NMV P142122, Pa element lateral view, × 45, SR245. N, NMV P142123, Pa element upper view, × 60, BON21–23. O, NMV P142124, Pa element lateral view, × 45, BON21–23. P, NMV P142125, Pa element lateral view, × 80, SR257. Q, NMV P142126, Pa element lateral view, × 45, SR245.

more even denticles, and the ear-shaped lobes of the basal cavity of *O. pseudomiae* are confined to the anterior half of the posterior portion of the blade. The lobes of the basal cavity of *Pand. s. miae* are heart-shaped and extend as a groove almost to the posterior of the blade. The denticles of *O. buchanensis* are much more irregular in size than those of *O. pseudomiae*, and the basal cavity is more centrally situated in *O. buchanensis*.

Ozarkodina linearis (Philip)

Fig. 12A–J

Discussion. Pathological conodont forms are frequently noted in collections but are rarely figured in publications. Three Sa elements of *O. linearis* are illustrated herein. One (Fig. 12H) is a normal specimen and two (Fig. 12I, J) are pathological forms. Weddige (1990) has suggested that such forms represent adverse conditions for the conodont animal, especially adverse feeding conditions. The distribution of forms exhibiting deformities may therefore cast some light on environmental pressures at the time. Weddige (1990: 568–572) has proposed a formal system for different types of "pathologies". If Weddige's scheme is followed, the two Sa elements of *O. linearis* in Figs 12I and 12J represent examples of duplicato pathology. Compared with a normal Sa element of the same species (Fig. 12H), these two specimens have a split or duplicate main denticle. It should be noted that most instances of duplication illustrated by Weddige (1990) are Early Devonian and occur predominantly in "spathognathodontan" apparatuses.

Genus Polygnathus Hinde, 1879

Type species. Polygnathus dubius Hinde, 1879.

Discussion. See Klapper (in Ziegler 1973) for discussion of the genus. During the past two dec-

ades there has been considerable discussion on the origin of polygnathids. Klapper & Philip (1972), Klapper & Johnson (1975) and Cooper (1973) favoured derivation from *Eognathodus*, whereas Lane & Ormiston (1979) and Sweet (1988) regarded *Ozarkodina* as the probable root stock for the polygnathids. The fauna from Boulder Flat adds strength to the argument for derivation from *Eognathodus*.

Polygnathus pireneae Boersma

Fig. 7A–F

Polygnathus lenzi Klapper.—Uyeno in McGregor & Uyeno 1972: pl. 5, figs 10–12 [Pa element].
Polygnathus n. sp.—Lane & Ormiston 1973: 330 [Pa element, not figured].
Polygnathus pireneae Boersma 1974: 287–288, pl. 2, figs 1–12 [Pa element].—Klapper in Ziegler 1977: 489–490, *Polygnathus* pl. 8, fig. 6 [Pa element].— Lane & Ormiston 1979: 62, pl. 3, figs 15–17, pl. 5, figs 2, 3, 9, 10, 27–34, 37 [Pa elements].—Klapper & Johnson 1980: 454 [Pa element].—Murphy & Matti 1982: 39–41, pl. 1, figs 33–38 [Pa elements].— Savage, Blodgett & Jaeger 1985: pl. 1, figs 21–26 [Pa elements].—Hou et al. 1988: 316–317, pl. 119, fig. 1 [Pa element].—Yolkin et al. 1989: 238, pl. 1, figs 1– 6 [Pa elements].—Valenzuela Rios 1990: 62 [Pa element, not figured].
Polygnathus n. sp. R.—Al Rawi 1977: 57–58, pl. 5, fig. 47 [Pa element].
non *Polygnathus pireneae.*—Bischoff & Argent 1990: pl. 3, fig. 14 [Pa element].

Discussion. Murphy & Matti (1982) drew attention to the very small size of Boersma's specimens from the Spanish Central Pyrenees, noting the possibility for larger specimens to show development of adcarinal grooves. The smallest *P. pireneae* recovered from low in the CABL section is 0.7 mm in length (Fig. 7A, B) compared to only 0.42mm for the holotype (Boersma 1974, pl. 2, figs 1–3). Larger specimens from CABL, for example the specimen illustrated in Fig. 7E–F, measuring 0.9mm in length, show the development of adcarinal grooves on the anterior portion of the platform.

→

Fig. 11. A–Q, *Ozarkodina pseudomiae* n. sp. A, NMV P142127, Pa element lateral view, × 60, SL28. B, NMV P142128, Pa element lateral view of holotype, × 60, SL28. C, NMV P142129, Pa element lateral view, × 45, SL32. D, NMV P142130, Pa element lateral view, × 60, SL29.5. E, NMV P142131, Pa element lateral view, × 45, SL27. F, NMV P142132, Pa element lateral view, × 45, SL32. G, NMV P142133, Pa element lateral view, × 45, SL60. H, NMV P142134, Pa element lateral view, × 45, SL33. I, L, NMV P142135, Pa element upper and lower views, × 45, CABL79.7 J, NMV P142136, Pa element lower view, × 50, CABL78.5. K, NMV P142137, Pa element upper view, × 50, SL52. M, NMV P142138, M element lateral view, × 60, SL33.5. N, NMV P142139, M element lateral view, × 70, SL33. O, NMV P142140, Pb element lateral view, × 60, SL28. P, NMV P142141, Se element lateral view, × 30, SL32. Q, NMV P142142, Se element lateral view, × 60, SL33.5. R, *Pandorinellina exigua philipi* (Klapper), NMV P142143, Pa element lateral view, × 60, CABL67.6. S, *Ozarkodina selfi* Lane & Ormiston, NMV P142144, Pa element lateral view, × 60, CABL80.6.
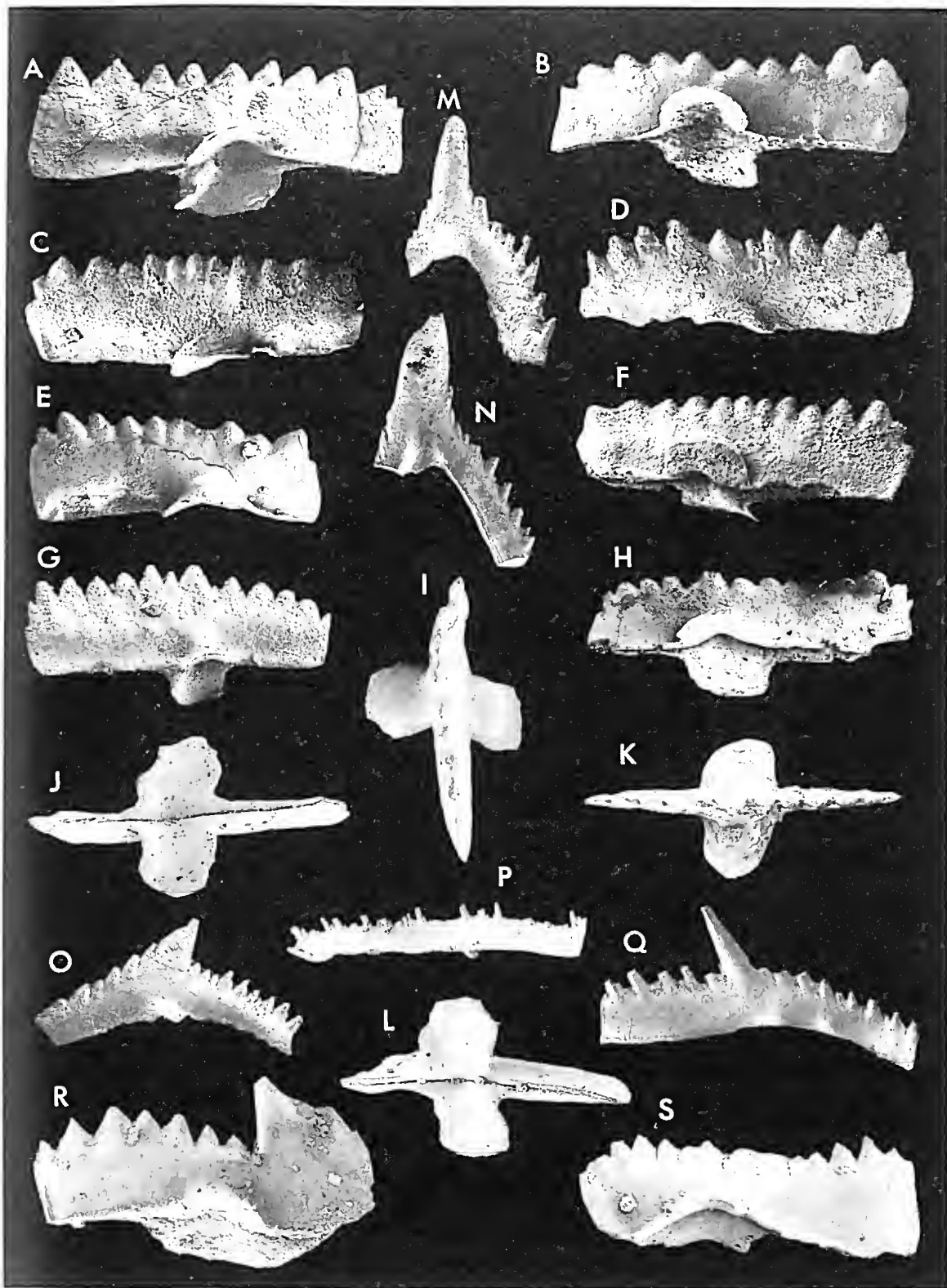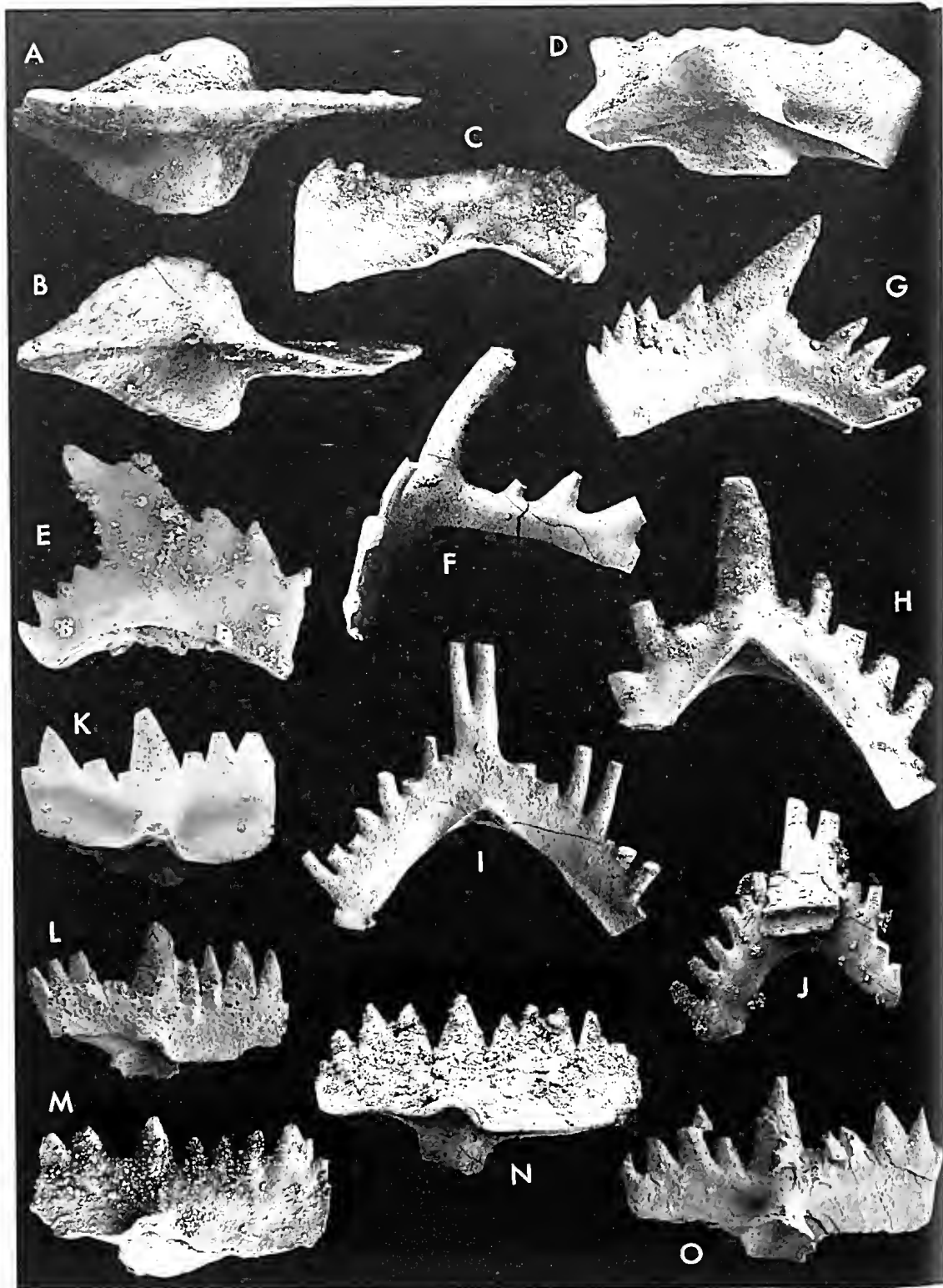
The position of *P. boucoti* Savage, 1977 is somewhat enigmatic. Although Lane & Ormiston (1979: 62), Klapper (in Klapper & Johnson 1980: 454) and Bischoff & Argent (1990: 459) considered it to be a junior synonym of *P. pireneae*, it is not synonymised with that species here. If Savage's illustrations of *P. boucoti* are compared with those of the slightly smaller holotype of *P. pireneae* (0.5mm compared with 0.42mm), there are three salient differences: the proportion of blade to platform is much greater in *P. boucoti*, the platform is poorly developed in *P. boucoti* and, in lateral view, *P. boucoti* is high anteriorly, gradually decreasing in height posteriorly, whereas in *P. pireneae* the height of the unit is relatively uniform.

Yolkin et al. (1989) distinguished two forms of *P. pireneae*, A and B, both with large flaring basal cavities and Form B with a flattened upper surface. As both features are reminiscent of *P. trilinearis* (see below), it could be that *P. trilinearis* gave rise to what to date has been considered the earliest stock of the polygnathids, *P. pireneae*.

Polygnathus cf. pireneae Boersma

Fig. 9H

Discussion. Five polygnathids from Boulder Flat (Table 6) are compared with *P. pireneae*; none is complete. Although occurring in samples with *P. trilinearis*, these specimens are much narrower in proportion to their length. Compare, for example, *P. trilinearis* in Fig. 9C–D with *P.* cf. *pireneae* in Fig. 9H. Note that the specimens are of similar length. More complete specimens are required for unequivocal determination.

Polygnathus trilinearis (Cooper)

Fig. 9A–G

Spathognathodus trilinearis Cooper 1973: 79, pl. 3, figs 1, 6, 7 [Pa element].
Eognathodus trilinearis.—Klapper in Ziegler 1977: 123, *Eognathodus* pl. 1, fig. 4 [Pa element].

Discussion. Eleven polygnathids are referred to *P. trilinearis*, ten from Boulder Flat and one from locality 92 at Tabberabbera (Table 6).

In evolutionary lineages, novelty of a feature generally heralds the incoming of a new species or genus. Instance the first appearance of irregularity of denticles in the *Ozarkodina pandora–Eognathodus sulcatus* lineage (Murphy 1989) where a slight irregularity and non-alignment of the denticles is indicative of the incoming of *E. sulcatus eosulcatus* Murphy. In assigning *"S". trilinearis* to *Polygnathus*, the introduction of a third row of denticles on the oral surface is taken as the novel feature distinguishing an eognathodid from a polygnathid. According to Clark et al. (1981) and Sweet (1988), *Eognathodus* is characterised by having a double row of denticles, one row extending from the posterior to the anterior and forming the free blade anteriorly. A species diverging from this pattern by developing a third row of denticles and having a blade confluent with the central row of denticles should not be assigned to *Eognathodus*.

Cooper (1973) referred four well preserved specimens to *"Spathognathodus" trilinearis*, noting that the two principal differences between *"S". trilinearis* and the earliest polygnathids were: (a) the "continuity of the anterior blade with one of the outer rows of nodes on the platform"; and (b) the "prominent flaring lobes surrounding the basal cavity".

(a) Examination of the fifteen specimens from Boulder Flat and the one specimen from Tabberabbera has shown that the first difference between early polygnathids and *"S". trilinearis* is not always manifest. Though it is apparent that some specimens show continuity of the free blade with an outside row of nodes (e.g. Cooper 1973, pl. 3, fig. 6, and Fig. 9F herein), this is not always the case. In Fig. 9E (herein) it can be seen that the blade passes into the central row of nodes. This feature, therefore, appears to be an unstable feature and not one on which genera should be separated.

←

Fig. 12. A–J, *Ozarkodina linearis* (Philip). A, B, NMV P142145, Pa element upper and lower views, × 45, SR129. C, NMV P142146, Pa element lateral view, × 35, SR129. D, NMV P142147, Pa element lateral view, × 45, SR190. E, NMV P142148, Pb element lateral view, × 60, CABL88. F, NMV P142149, Se element lateral view, × 45, SR106.8. G, NMV P142150, Pb element lateral view, × 35, SR214.5. H, NMV P142151, Sa element lateral view, × 45, SR256.5. I, NMV P142152, Sa element, example of Duplicato Pathology *sensu* Weddige (1990), × 45, SR129. J, NMV P142153, Sa element, example of Duplicato Pathology *sensu* Weddige (1990), × 60, SR214.5. K–O, *Ozarkodina buchanensis* (Philip). K, NMV P142154, Pa element lateral view of juvenile specimen, × 100, CABL55. L, NMV P142155, Pa element lateral view, × 60, SL29.5. M, NMV P142156, Pa element lateral view, × 50, SR245. N, NMV P142157, Pa element lateral view, × 70, SR125. O, NMV P142158, Pa element lateral view, × 50, SL38.5.
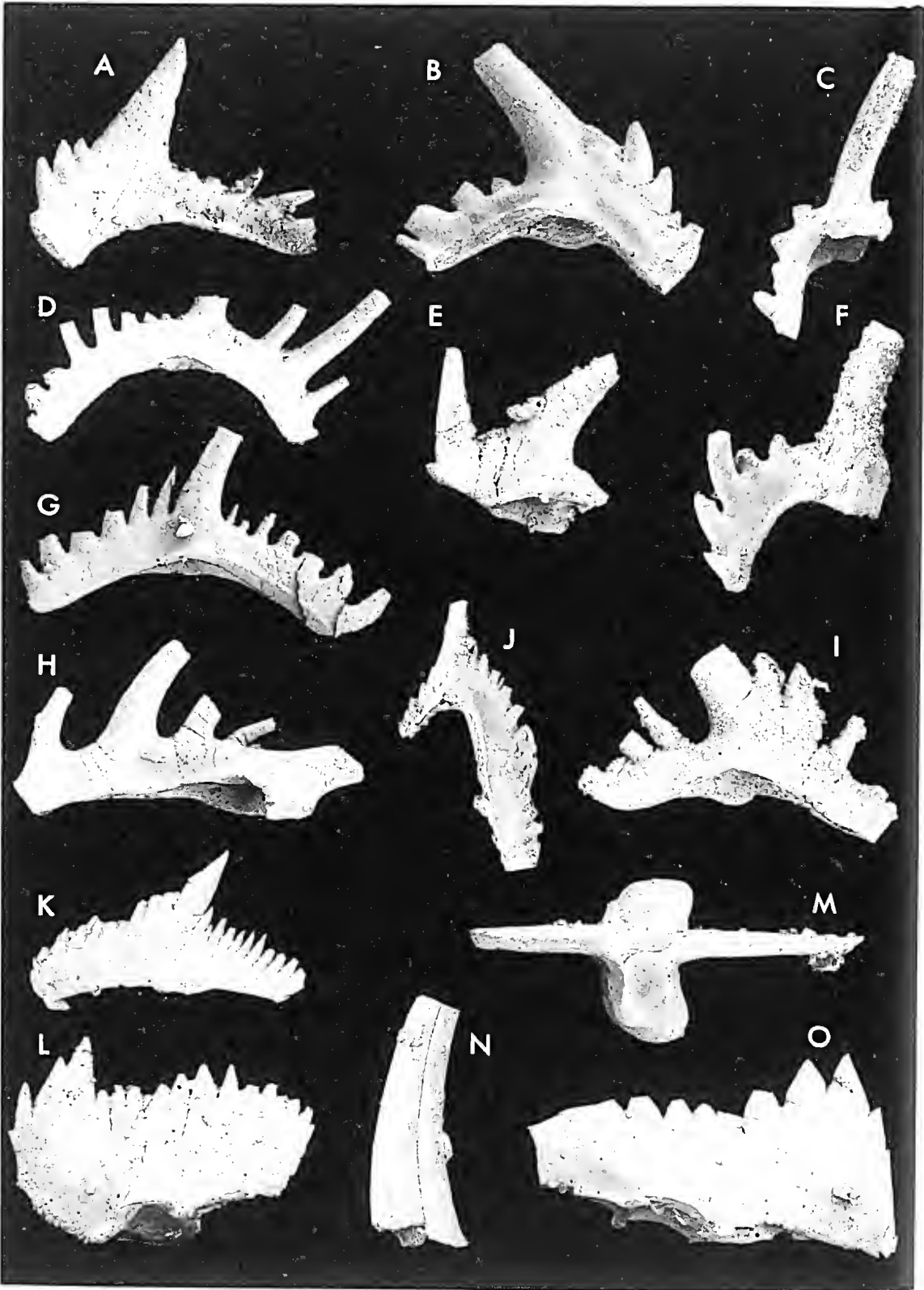
(b) By definition (Clark et al. 1981), the Pa elements of both *Eognathodus* and *Polygnathus* are carminiscaphate, i.e. having a capacious basal cavity; the "prominent flaring lobes surrounding the basal cavity" noted by Cooper (1973), therefore, pose no problem to placing *"S". trilinearis* in *Polygnathus*.

Lane & Ormiston (1979) suggested that Cooper's (1973) *"S". trilinearis* could be an aberrant form of *P. pireneae*. The former is now known from four localities: Loyola, Tabberabbera and Boulder Flat in Victoria, and associated with indubitable *P. pireneae* in a clast from the lower Cunningham Formation, 200 m stratigraphically beneath the Red Hill Limestone Member, 6.2 km north-north-west of Mumbil in allotment 65, parish of Mumbil, at grid reference 8732 I & IV Burrendong 90408325 in east-central New South Wales. Because of consistent morphology throughout the occurrences known to us we are convinced that *P. trilinearis* and *P. pireneae* are discrete species.

ACKNOWLEDGEMENTS

REFERENCES

AL RAWI, D., 1977. Biostratigraphische Gliederung der Tentaculiten-Schichten des Frankenwaldes mit Conodonten und Tentaculiten (Unter-und Mittel-Devon; Bayern, Deutschland). *Senckenbergiana lethaea* 58: 25–79.

ANDREWS, E. C., 1938. The structural history of Australia during the Palaeozoic (The stabilization of a continent). *Journal of the Royal Society of New South Wales* 71: 118–187.

ARGENT, J. C., 1971. Stratigraphy and conodont biozonation of Lower Devonian limestones, Waratah Bay, Victoria. BA (Hons) thesis, Macquarie University.

BISCHOFF, G. C. O. & ARGENT, J. C., 1990. Lower Devonian (Late Lochkovian–Pragian) limestone stratigraphy at [sic!] conodont distribution, Waratah Bay, Victoria. *Courier Forschungsinstitut Senckenberg* 118: 441–471.

BOERSMA, K. T., 1974. Description of certain Lower Devonian platform conodonts of the Spanish central Pyrenees. *Leidse geologische Mededelingen* 49: 285–301.

BRADLEY, K., 1969. Geology of the Murrindal River–Yalmy River area east of Buchan, Victoria. *Proceedings of the Royal Society of Victoria* 82: 277–285.

BROWNE, I. A., 1959. Stratigraphy and structure of the Devonian rocks of the Taemas and Cavan area, Murrumbidgee River, south of Yass, NSW. *Journal and Proceedings of the Royal Society of New South Wales* 92: 115–128.

BULTYNCK, P., 1989. Conodonts from the La Grange Limestone (Emsian), Armorican Massif, northwestern France. *Courier Forschungsinstitut Senckenberg* 117: 173–203.

CLARK, D. L., SWEET, W. C., BERGSTROM, S. M., KLAPPER, G., AUSTIN, R. A., RHODES, F. H. T., MULLER, K. G., ZIEGLER, W., LINDSTROM, M., MILLER, J. F. & HARRIS, A. G., 1981. *Treatise on Invertebrate Paleontology*, Part W, *Miscellanea*, Supplement 2, *Conodonta*. Geological

Fig. 13. A, E, *Oulodus* sp. A. A, NMV P142159, Pa element, × 50, CABL72.5. E, NMV P142160, ?M element, × 60, CABL131.7. B–D, F, H, *Oulodus* sp. B. B, NMV P142161, Pa element, × 40, CABL71. C, NMV P142162, M element, × 20, CABL73.4. D, NMV P142163, Pb element, × 60, CABL84. F, NMV P142164, Se element, × 50, CABL73.4. H, NMV P142165, ?Sb element, × 60, CABL131.7. G, *Oulodus* sp. C, NMV P142166, Pa element, × 50, TAB97. I, *Oulodus* sp. D, NMV P142167, Pa element, × 45, CABL129. J–L, *Ozarkodina* cf. *optima* (Moskalenko). J, NMV P142168, M element, × 60, TAB52. K, NMV P142169, Pb element, × 55, TAB97. L, NMV P142170, Pa element, × 60, TAB92. M, *Pandorinellina steinhornensis steinhornensis* (Ziegler), NMV P142171, Pa element, × 40, TAB97. N, *Neopanderodus aequabilis* Telford, NMV P142172, × 75, TAB52. O, *Pandorinellina exigua philipi* (Klapper), NMV P142173, Pa element, × 50, TAB97.

Society of America, Inc. and University of Kansas, Boulder, Colorado, and Lawrence, Kansas, 202 p.

CONAGHAN, P. J., MOUNTJOY, E. J., EDGECOMBE, D. R., TALENT, J. A. & OWEN, D. E., 1976. Nubrigyn algal reefs (Devonian), eastern Australia: allochthonous blocks and megabreccias. *Bulletin of the Geological Society of America* 87: 515–530.

COOPER, B. J., 1973. Lower Devonian conodonts from Loyola, Victoria. *Proceedings of the Royal Society of Victoria* 86: 77–84, pls 2, 3.

CRAMSIE, J. N., POGSON, D. J. & BAKER, G. J., 1975. Yass 1:100,000 geological sheet. Geological Survey of New South Wales.

CRAMSIE, J. N., POGSON, D. J. & BAKER, G. J., 1979. *Geology of the Yass 1:100,000 Sheet.* Geological Survey of New South Wales, 85 p.

EASTON, J. G., 1938. The geology and physiography of the Mitchell River Gorge. *Mining and Geological Journal (Victoria)* 1 (3): 73–75.

FLETCHER, K., 1963. The Snowy River Volcanics west of Buchan, Victoria. *Proceedings of the Royal Society of Victoria* 76: 169–179, pl. 20.

HILL, D., 1950. Middle Devonian corals from the Buchan district, Victoria. *Proceedings of the Royal Society of Victoria* 62: 137–164, pls 5–9.

HILL, D., 1954. Devonian corals from Waratah Bay, Victoria. *Proceedings of the Royal Society of Victoria* 66: 105–118, pls 6–9.

HOU HONG-FEI ET AL. (eds), 1988. *Devonian Stratigraphy, Paleontology and Sedimentary Facies of Longmenshan, Sichuan.* Geological Publishing House, Beijing, 487 p., 184 pls.

JOHNSON, J. G., KLAPPER, G. & SANDBERG, C. A., 1985. Devonian eustatic fluctuations in Euramerica. *Bulletin of the Geological Society of America* 96: 567–587.

KLAPPER, G., 1977. Lower and Middle Devonian conodont sequence in central Nevada; with contributions by D. B. Johnson. *University of California Riverside, Campus Museum Contributions* 4: 33–54.

KLAPPER, G, & JOHNSON, J. G., 1975. Sequence in conodont genus *Polygnathus* in Lower Devonian at Lone Mountain, Nevada. *Geologica et Palaeontologica* 9: 65–83.

KLAPPER, G. & JOHNSON, J. G., 1980. Endemism and dispersal of Devonian conodonts. *Journal of Paleontology* 54: 400–455.

KLAPPER, G. & PHILIP, G. M., 1971. Devonian conodont apparatuses and their vicarious skeletal elements. *Lethaia* 4: 429–452.

KLAPPER, G. & PHILIP, G. M., 1972. Familial classification of reconstructed Devonian conodont apparatuses. *Geologica et Palaeontologica* SB1: 97–113.

KRÖMMELBEIN, K., 1954. Devonische Ostrakoden aus der Gegend von Buchan und von der Küste der Waratah Bay. *Senckenbergiana lethaea* 35: 193–229, pls 1–5.

LANE, H. R. & ORMISTON, A. E., 1973. Biostratigraphy of the Salmontrout Limestone, east-central Alaska. *Geological Society of America, Abstracts with Programs* 5: 30.

LANE, H. R. & ORMISTON, A. E., 1979. Siluro-Devonian biostratigraphy of the Salmontrout River area, east-central Alaska. *Geologica et Palaeontologica* 13: 39–96, 12 pls.

McGREGOR, D. C. & UYENO, T. T., 1972. Devonian spores and conodonts of Melville and Bathurst Islands, District of Franklin. *Geological Survey of Canada Paper* 71-13: 1–37.

MAWSON, R., 1986. Early Devonian (Lochkovian) conodont faunas from Windellama, New South Wales. *Geologica et Palaeontologica* 20: 39–71

MAWSON, R., 1987a. Early Devonian conodont faunas from Buchan and Bindi, Victoria, Australia. *Palaeontology* 30: 251–297.

MAWSON, R., 1987b. Documentation of conodont assemblages across the Early Devonian–Middle Devonian boundary, Broken River Formation, North Queensland, Australia. *Courier Forschungsinstitut Senckenberg* 92: 251–273.

MAWSON, R. & TALENT, J. A., 1989. Late Emsian-Givetian stratigraphy and conodont biofacies—carbonate slope and offshore shoal to sheltered lagoon and nearshore carbonate ramp—Broken River, North Queensland, Australia. *Courier Forschungsinstitut Senckenberg* 117: 205–259.

MAWSON, R. & TALENT, J. A., 1992. Molong Platform and Hill End Trough (NSW) in the Early Devonian: a pattern of platform exposure and reciprocal carbonate sedimentation offshore. *Geological Society of Australia Abstracts* 32: 180.

MAWSON, R., TALENT, J. A., BEAR, V. C., BENSON, D. S., BROCK, G. A., FARRELL, J. R., HYLAND, K. A., PYEMONT, B. D., SLOAN, T. R., SORENTINO, L., STEWART, M. I., TROTTER, J. A., WILSON, G. A. & SIMPSON, A. G., 1988. Conodont data in relation to resolution of stage and zonal boundaries for the Devonian of Australia. *Memoir of the Canadian Society of Petroleum Geologists* 14: 485–527.

MAWSON, R., TALENT, J. A. & JELL, J. S., 1985. Stage boundaries within the Devonian: implicaitons for application to Australian sequences. *Courier Forschungsinstitut Senckenberg* 92: 251–273.

MAWSON, R., TALENT, J. A., ET AL., in prep. Age of Early Devonian submarine fan deposits and isolated limestone megaclasts, east-central Victoria.

MURPHY, M. A., 1989. Lower Pragian boundary (Lower Devonian) and its application in Nevada. *Courier Forschungsinstitut Senckenberg* 117: 61–70.

MURPHY, M. A. & MATTI, J. C., 1982. Lower Devonian conodonts (*hesperius–kindlei* Zones).

central Nevada. *University of California Publications of Geological Science* 123: 1–82.

OLIVER, W. A. & CHLUPÁC, I., 1991. Defining the Devonian: 1979–89. *Lethaia* 24: 119–122.

OWEN, M. & WYBORN, D., 1979. Geology and geochemistry of the Tantangara and Brindabella area. *Australia, Bureau of Mineral Resources, Geology and Geophysics, Bulletin* 204, 1–52.

PEDDER, A. E. H., 1967. The Devonian rocks of the Murrumbidgee River area, New South Wales. In *International Symposium on the Devonian System, Calgary, 1967*, vol. 2, D. H. Oswald, ed., Alberta Society of Petroleum Geologists, Calgary, 143–146.

PEDDER, A. E. H., JACKSON, J. H. & PHILIP, G. M., 1970. Lower Devonian biostratigraphy in the Wee Jasper region of New South Wales. *Journal of Paleontology* 44: 206–251, pls 37–50.

PHILIP, G. M., 1965. Lower Devonian conodonts from the Tyers area, Gippsland, Victoria. *Proceedings of the Royal Society of Victoria* 79: 95–117, pls 8–10.

PHILIP, G. M., 1966. Lower Devonian conodonts from the Buchan Group, eastern Victoria. *Micropaleontology* 12: 441–460.

PHILIP, G. M. & JACKSON, J. H., 1967. Lower Devonian subspecies of the conodont *Polygnathus linguiformis* Hinde from southeastern Australia. *Journal of Paleontology* 41: 1262–1266.

PHILIP, G. M. & PEDDER, A. E. H., 1964. A re-assessment of the age of the Middle Devonian of south-eastern Australia. *Nature* 202: 1323–1324.

PHILIP G. M. & PEDDER, A. E. H., 1967a. The age of the Lilydale Limestone (Devonian), Victoria. *Journal of Paleontology* 41: 795–798.

PHILIP, G. M. & PEDDER, A. E. H., 1967b. A correlation of some Devonian limestones of New South Wales and Victoria. *Geological Magazine* 104: 232–239.

PHILIP, G. M. & PEDDER, A. E. H., 1967c. Stratigraphical correlation of the principal Devonian limestone sequences of eastern Australia. In *International Symposium on the Devonian System, Calgary, 1967*, vol. 2, D. H. Oswald, ed., Alberta Society of Petroleum Geologists, Calgary, 1025–1041.

PICKETT, J. W., 1978. Conodont faunas from the Mount Frome Limestone (Emsian–Eifelian), New South Wales. *Australia, Bureau of Mineral Resources, Geology and Geophysics, Bulletin* 192: 97–107.

PICKETT, J. W., 1980. Conodont assemblages from the Cobar Supergroup (Early Devonian), New South Wales. *Alcheringa* 4: 67–88.

PICKETT, J. W., 1984. The age of the Boulder Flat limestone, near Combienbar, Victoria. *Geological Survey of New South Wales Report* 84/8, 1 p.

RAMSEY, W. R. H. & VANDENBERG, A. H. M., 1986. Metallogeny and tectonic development of the Tasman Fold Belt System in Victoria. *Ore Geology Reviews* 1: 213–257.

RIPPER, E. A., 1937. On the stromatoporoids of the Buchan district, Victoria. *Proceedings of the Royal Society of Victoria* 50: 11–38, pls 2–5.

SAVAGE, N. M., 1977. Lower Devonian conodonts from the Gazelle Formation, Klamath Mountains, northern California. *Journal of Paleontology* 51: 57–62.

SAVAGE, N. M., BLODGETT, R. B. & JAEGER, H., 1985. Conodonts and associated graptolites from the late Early Devonian of east-central Alaska and western Yukon Territory. *Canadian Journal of Earth Sciences* 22: 1880–1883.

SPARLING, D. R., 1984. Paleoecologic and paleogeographic factors in the distribution of lower Middle Devonian conodonts from north-central Ohio. *Geological Society of America Special Paper* 196: 113–125.

SWEET, W. C., 1988. *The Conodonta: Morphology, Taxonomy, Paleoecology and Evolutionary History of a Long-Extinct Animal Phylum.* (Oxford Monographs on Geology and Geophysics No. 10), 212 p.

TALENT, J. A., 1955. Devonian sediments at Waratah Bay. Frome–Lakes Pty Ltd, Melbourne, Report 5G, 38 p.

TALENT, J. A., 1956. Devonian brachiopods and pelecypods of the Buchan Caves Limestone, Victoria. *Proceedings of the Royal Society of Victoria* 68: 1–56, pls 1–5.

TALENT, J. A., 1963. The Devonian of the Mitchell and Wentworth rivers. *Memoir of the Geological Survey of Victoria* 24: 1–118, pls 1–78.

TALENT, J. A., 1965. The stratigraphic and diastrophic evolution of central and eastern Victoria in Middle Palaeozoic times. *Proceedings of the Royal Society of Victoria* 79: 179–195.

TALENT, J. A., 1967. Eastern Victoria. In *Australia-New Zealand Association for the Advancement of Science, Excursion Handbook*, Section C, 69–85.

TALENT, J. A., 1969. Geology of East Gippsland. *Proceedings of the Royal Society of Victoria* 82: 37–60.

TALENT, J. A., 1985. Devonian zoogeography in relation to tectonics and suspect terranes in eastern Australia. In *Third Circum-Pacific Terrane Conference*, E. Leitch, ed., Geological Society of Australia, Sydney, 228–233.

TALENT, J. A., 1988. Organic reef-building: episodes of extinction and symbiosis? *Senckenbergiana lethaea* 69: 315–368.

TALENT, J. A., 1989. Transgression-regression pattern for the Silurian and Devonian of Australia. In *Pathways in Geology—Essays in Honour of Edwin Sherbon Hills*, R. W. Le Maitre, ed., 201–219. Distributed by Blackwells, Carlton.

TALENT, J. A. & MAWSON, R., in prep. Molong Platform and adjacent Hill End Trough (New South Wales) in the Early Devonian: conodont data in relation to patterns of platform exposure, tec-

tonics, and coeval carbonate sedimentation off-
shore.

TALENT, J. A. & YOLKIN, E. A., 1987. Transgression-
regression patterns for the Devonian of Aus-
tralia and southern West Siberia. *Courier
Forschungsinstitut Senckenberg* 92: 235–249.

TEICHERT, C., 1954. Note on Devonian limestones
between The Bluff and Bird Rock, Waratah
Bay, Victoria. *Proceedings of the Royal Society
of Victoria* 66: 103–104.

TEICHERT, C. & GLENISTER, B. F., 1952. Fossil nauti-
loid faunas from Australia. *Journal of Paleon-
tology* 26: 730–752, pls 104–108.

TEICHERT, C. & TALENT, J. A., 1958. Geology of the
Buchan area, East Gippsland. *Memoir of the
Geological Survey of Victoria* 21: 1–56, pls
1–7.

THOMAS, D. E., 1949. Limestone at Errinundra.
Mining and Geological Journal (Victoria) 3 (5):
24–26.

VALENZUELA-RIOS, J. I., 1990. Lochkovian conodonts
and stratigraphy at Gerrida de La Sal (Pyren-
ees). *Courier Forschungsinstitut Senckenberg*
118: 53–63.

VANDENBERG, A. H. M., 1988. Silurian–Middle De-
vonian. In *Geology of Victoria*, 2nd edn, J. G.
Douglas & J. A. Ferguson, eds, Victorian Div-
ision, Geological Society of Australia, 103–
146.

VANDENBERG, A. H. M., BOLGER, P. F., CAREY, S. P.,
O'SHEA, P. J. & NOTT, R. J., 1981. Limestone
Creek 1:50,000 geological map. Geological Sur-
vey of Victoria.

VANDENBERG, A. H. M., BOLGER, P. F. & O'SHEA. P.
J., 1984. Geology and mineral exploration of
the Limestone Creek area, northeast Victoria.
*Department of Minerals and Energy (Victoria)
Geological Survey Report* 72: 1–59.

VANDENBERG, A. H. M., NOTT, R. J., ROBERTS, P. S.,
KING, R. L. & ORTH, K., 1990. Bendoc (8623
Zone 55) 1:100,000 geological map. Depart-
ment of Industry and Office of Planning, Vic-
toria.

WEBB, J. A., 1992. Early Devonian sequence strati-
graphy from Buchan and Bindi, eastern Vic-
toria. *Geological Society of Australia Abstracts*
32: 112–113.

WEDDIGE, K., 1990. Pathological conodonts. *Courier
Forschungsinstitut Senckenberg* 118: 563–589.

WHITELAW, H. S., 1954. Some limestone and marble
deposits of East Gippsland. *Mining and Geo-
logical Journal (Victoria)* 5 (3): 23–33.

YOLKIN, E. A., APEKINA, L. S., ERINA, M. V., IZOKH,
N. G., KIM, A. I., TALENT, J. A., WALLISER, O.
H., WEDDIGE, K., WERNER, R. & ZIEGLER, W.,
1989. Polygnathid lineages across the Pragian-
Emsian boundary, Zinzilban Gorge, Zerafshan,
USSR. *Courier Forschungsinstitut Senckenberg*
110: 237–246.

ZIEGLER, W. (ed.), 1973. *Catalogue of Conodonts*, vol.
1, E. Schweizerbart'sche Verlagsbuchhandlung,
Stuttgart, 504 p., 27 pls.

ZIEGLER, W. (ed.), 1977. *Catalogue of Conodonts*, vol.
3, E. Schweizerbart'sche Verlagsbuchhandlung,
Stuttgart, 574 p., 39 pls.

A REVIEW OF SCIENTIFIC STUDIES AND THE MANAGEMENT OF NUTRIENT LOADS TO PORT PHILLIP BAY

A. W. CHIFFINGS, A. J. BREMNER AND V. B. BROWN

Melbourne Water, PO Box 4342, Melbourne, Victoria 3001

The history of the nutrient enrichment of Port Phillip Bay is very much the history of the growth of Melbourne and of the support services developed to manage the collection, treatment and disposal of sewage and industrial wastes. This history is briefly summarised, as is that of the major scientific studies undertaken on Port Phillip Bay. The need to improve our understanding of how Melbourne as a city impacts on the marine environment is seen as an essential part of the on-going program of planning and managing the city's waste disposal system.

PORT PHILLIP BAY, a large, shallow marine embayment with restricted exchange to Bass Strait, is an integral part of the Melbourne environment and represents a major asset which is important to the prosperity and well-being of the city as well as to the rest of the State. The Bay is important because of the opportunities it offers in terms of recreation, tourism, commercial fishing, mariculture, transport and shipping, urban scenic value, cooling water, and as a receiving environment for urban and industrial wastes and dredge spoil. The economic worth of the Bay is illustrated in a simple way by the following figures for the value of its fisheries (Bremner et al. 1989).

Commercial fishing	$50–80 million	(1986)
Recreational fishing	$250 million	(1982)

The disposal to the Bay of sewage, other domestic waste and dredge spoil is not recognized as a "beneficial use" under the Victorian Environment Protection Act. Nevertheless, the development of the city and its adjacent suburban and industrial assets over the last 160 years has taken place by using the Bay as a cost-effective mechanism for the disposal of waste materials. The wastes include plant nutrients which, when present in "excess", have been shown to cause major changes in water quality and biological systems (e.g. Cambridge 1975, Cambridge et al. 1986, Silberstein et al. 1986, Chiffings & McComb 1981, Simpson et al. 1990). The capacity of the Bay to continue to assimilate or accommodate these materials is a key question that needs to be addressed in future scientific assessments of the Bay.

MELBOURNE'S IMPACT ON THE BAY

Prior to settlement of the region by Europeans, inputs of nutrients to the Bay from land-based sources would have been part of a natural process of addition, recycling and loss that occurs in all coastal waters. These processes in conjunction with natural physical and biological characteristics would have dictated the net productivity of Port Phillip Bay.

The process of nutrient addition has now been greatly enhanced by urban, industrial and agricultural activities within the catchment over the last 150 years. In a developed catchment, plant nutrients come from sewerage discharges, urban run-off, clearing of the catchment, agricultural activities, emergency sewerage overflows, unsewered properties and industrial wastes. Depending on the degree of increase in net production prompted by the addition of nutrients from such sources, the effects on a coastal system may be beneficial or detrimental (Mann 1982). The history of this "cultural" nutrient enrichment of Port Phillip Bay reflects the history of the growth of Melbourne itself.

The settlement on the banks of the Yarra had a resident population of some 200 when it was named Melbourne by Governor Bourke in March 1837 (Grant & Serle 1983). Melbourne's subsequent growth was rapid and by 1841 the population was estimated at 6,000. The Yarra was both water supply and sewer, and the town became notorious world-wide for its high death rate through cholera and dysentery. By 1858 the problem of water supply had been addressed with the construction of Melbourne's first dam

at Yan Yean on the Plenty River (Dingle & Rasmussen 1992).

Sanitary conditions in the town were very poor, as reflected by a survey undertaken by Clement Hodgkinson in 1852 for a Select Committee on the Sewerage and Supply of Water for Melbourne. He found that "in backyards and enclosures, more astounding accumulations of putrescent substances and rubbish of all kinds, than I ever inspected in the very worst parts of dirtiest English and Continental towns... Many of the foundations of the buildings were greatly injured owing to the saturation of the subsoil by liquid excrementitious matter" (Grant & Serle 1983). This situation, combined with the establishment of tallow rendering plants on the banks of the Yarra, led to a severe degradation of the water quality of the river (Seeger 1961) and, presumably, of parts of the Bay.

Such conditions prevailed for an additional 45 years before the Melbourne sewerage system was commissioned by the Melbourne and Metropolitan Board of Works (MMBW, now Melbourne Water), established in 1891. By 1899, the population of Melbourne was estimated at 477,790 and 32% of the 105,000 tenements were connected to the sewerage system (Seeger 1961).

The rate of progress in sewering Melbourne over the intervening 93 years varied, with a consequent impact on the water quality of Melbourne's urban streams and the Bay. As recently as 1970 the Senate Select Committee on Water Pollution documented an extremely poor situation in and around Melbourne, with ambient water quality influenced by sewerage and industrial waste discharges. Since then, progressive action has ensured considerable improvements in the water quality of urban streams (Bremner et al. 1989). These improvements are due to State initiatives resulting in the establishment of the Victorian Environment Protection Authority (EPA), and to the National Sewerage Program established by the Federal Government in the 1970s. A total of $88,290,816 (historic dollar values) was spent by Melbourne Water from the National Sewerage Program over the period 1973–77, leading to a considerable decrease in the backlog of properties to be sewered.

The introduction of EPA licence requirements for discharges to waterways and drains also had an impact, leading to improvements in discharge quality, the termination of discharges, or their diversion to the sewer. In their role as a delegated agency for the EPA, Melbourne Water used data from Phase 1 of the Environmental Study of Port Phillip Bay (see below) in setting licence conditions for discharges. The EPA used the physico-chemical data and recommendations from the study in preparing the State Environment Protection Policy (SEPP) for the Waters of Port Phillip Bay.

Although trade waste discharges were first accepted into the sewer in 1945, after the establishment of the EPA in 1970 there has been an increasing trend for industrial wastes to be diverted away from urban streams and the Bay and into the sewerage system. At present, trade waste discharges account for 17.5% of the average daily flow of 504 ML and 48% of the biochemical oxygen demand (BOD) load to the Werribee Treatment Complex (WTC; Fig. 1), which discharges the treated waste water to Port Phillip Bay. In contrast, trade waste discharges account for only 6.3% of the average daily flow of 361 ML and 21% of the BOD load to the Carrum Treatment Complex, which discharges to Bass Strait.

With an estimated resident population (at June 1990) of 2,585,000 living in 997,390 properties, 98% of which are connected to the sewerage system (MMBW 1990a), Melbourne now has a well-established hydraulic infrastructure for the management of its domestic wastes and much of its industrial wastes. Strong design principles laid down by James Mansergh in 1890 have led to this system having served the city for 100 years (Dingle & Rasmussen 1991). While considerable additions and improvements have been made to the original system in order to service the growth of Melbourne, much of it is still in use.

Principal features of the system are the use of land treatment located at a site consistent with the anticipated growth pattern and population of the metropolis, separation of surface drainage from sewage collection, and an initial investment in infra-structure which was designed to service a community of 1.7 million at a time when the population was less than 500,000. In June 1990 dollar values the initial capital investment in the system in 1900 was $198 million. In comparison, the worth of these capital assets as developed over the 90 year period was estimated in June 1990 at $1.8 billion (MMBW 1990a).

About 93% of the sewage flow from Melbourne was treated by the WTC system prior to the commissioning of the Carrum Treatment Complex in 1975. During 1988/89, approximately 179,000 ML or 60% of the annual flow from Melbourne was treated at Werribee. The facilities include treatment of 16% of the flow by
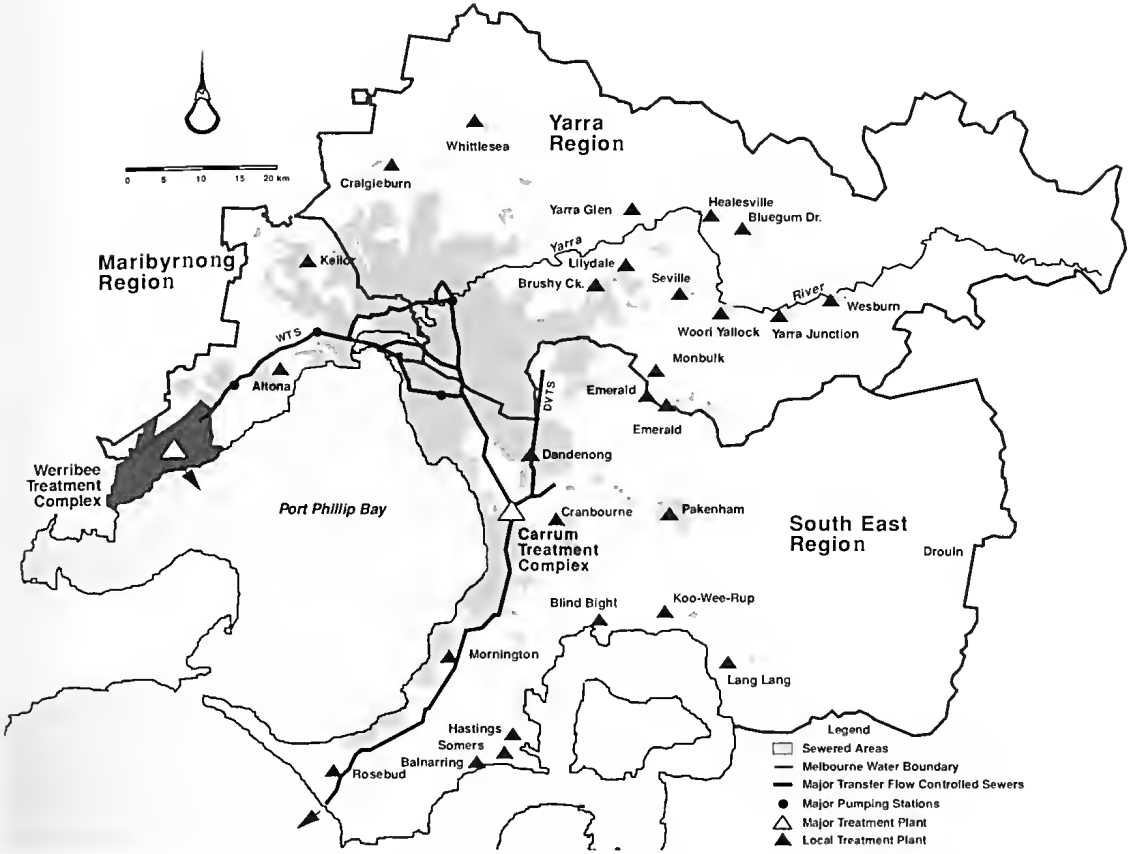
Fig. 1. Schematic plan of the Melbourne sewerage system showing the location of the major trunk sewers, treatment plants and outfalls. The Melbourne Water boundary for the provision of sewerage is also shown.

land filtration, 26% by grass filtration and 58% by lagoons (Croxford 1978, McPherson 1979, Bremner & Chiffings 1991).

Land treatment methods have been used at the WTC to process waste water since 1897, with the final effluent being discharged to Port Phillip Bay for the full 93 year period. We have estimated that a total volume of 9.6 billion ML of sewage has been received at the WTC over this period, during which the population of Melbourne has grown some six fold.

Present preliminary estimates have placed surface nutrient loads from WTC as ranging between 54% and 71% of the total surface loads to the Bay, depending on fluctuations in loads from some stream catchments (Fig. 2).

In addition, Port Phillip Bay receives nutrients from:

(a) Stormwater run-off from Melbourne and its suburbs via drains and input streams; e.g. the Yarra River and its urban drains;

(b) Surface and groundwater run-off from agricultural land in the river and stream catchments;

(c) Atmospheric sources, both particulate and in solution.

Aerial loadings are significant. Carnovale & Saunders (1988) estimated that a total of 0.8–1.3 kilotonnes of N are deposited to the Bay annually from these sources, equivalent to 20–32% of the N load from the WTC.

SCIENTIFIC STUDIES ON PORT PHILLIP BAY

First attempts to obtain a biological survey of the Bay came from the Council of the Royal Society of Victoria who in 1888 elected a Committee which was granted an initial sum of £50 (approximately $3,000 June 1990 equivalent) for the task. A full report of the committee's activities was given in the Society's 1890 Annual
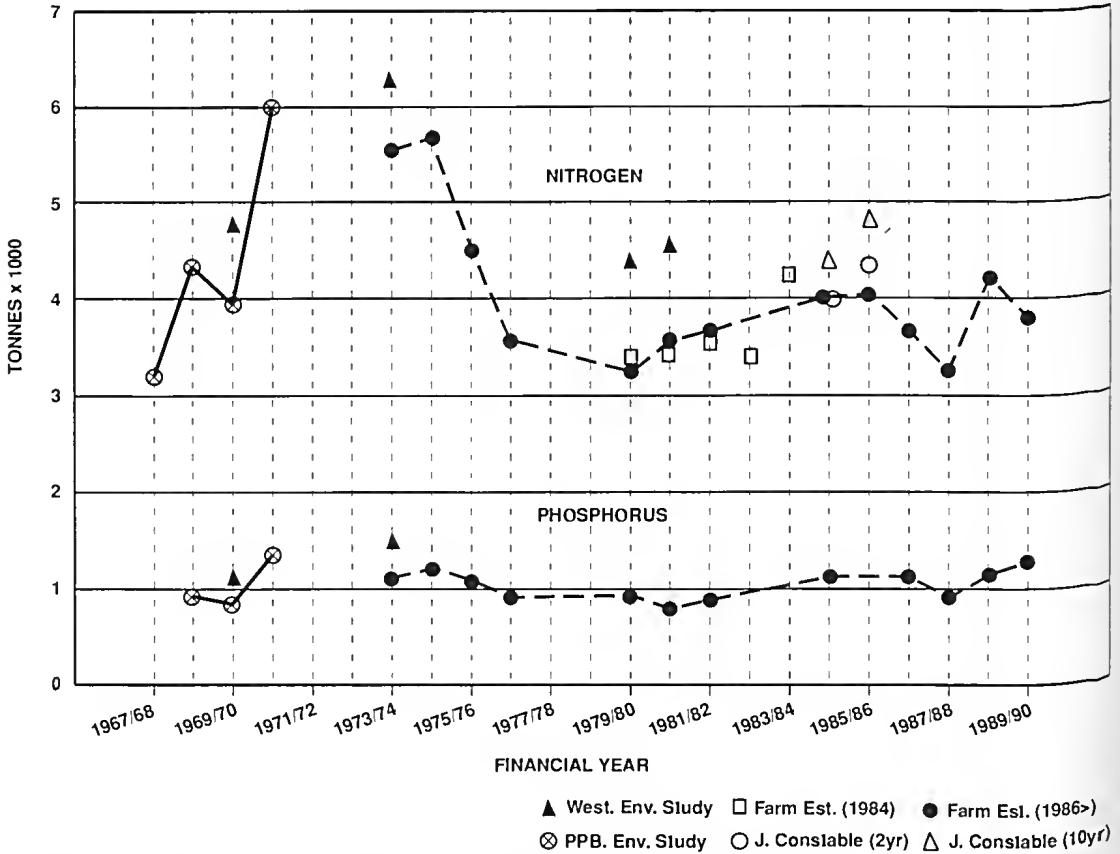
Fig. 2. Annual estimates of total nitrogen and total phosphorus loads discharged from the Werribee Treatment Complex to Port Phillip Bay over the last 20 years. Details of how estimates were derived are given in the Appendix.

Report. The work concentrated on specific taxonomic groups and several monographs were produced, but by 1896 the Society's records did not reflect any on-going work (Macpherson & Lynch 1966). While recognizing the considerable advances made in the collection, taxonomy and naming of species in recent years, a review of this very early work may provide insights into the impact of European settlement on the Bay over the last 100 years.

The first attempt at gaining a systems oversight into the Bay was undertaken by D. J. Rochford between 1947 and 1952 as part of an Australia-wide investigation of the physical processes of coastal embayments and estuaries. Data on chlorinity, temperature, nitrate nitrogen, inorganic phosphates and oxygen were collected from 6 stations around the Bay (Rochford 1966).

No other systematic attempt was made to study the Bay until 1957 when a five-year joint project was undertaken by the National Museum of Victoria and the Fisheries and Wildlife Department, the aim being "... to record the macro flora and fauna and to plot its distribution and where possible at least make an assessment of the density of the population present" (Macpherson & Lynch 1966). The results, published in *Memoirs of the National Museum of Victoria* volumes 27 (1966) and 32 (1971), included papers on geology, geomorphology, bottom sediments, and hydrology (Rochford's work), fisheries and various taxonomic groups. With the exception of Rochford's work, these studies did not assess water quality of the Bay or the overall state of its biological communities.

During 1968–71 the MMBW and the Fisheries and Wildlife Department jointly conducted the first comprehensive environmental study of the Bay and its catchment, in order to determine the relationships between prevailing inputs and conditions in the Bay (*Environment*

tal Study of Port Phillip Bay Phase I). The study was to also collect baseline data in the vicinity of the outfall of the proposed south-eastern system sewage treatment plant at Carrum, which was designed to discharge effluent into the Bay for the first ten years of its life, at a site approximately 3.2 km offshore from the Paterson River. The need to address the possible impact of the sewerage discharge was abdicated when in early 1969 the State Government directed that a pipeline to Bass Strait should be included in the construction of the plant (Dingle & Rasmussen 1991). The study continued, however, and was the first of several such studies undertaken in Victoria on different water bodies.

The results of the Phase I Study were summarised in a single publication (MMBW/FWD 1973) but the original data were never collated and many of them have been lost, defeating one of the principal objectives of the study.

For nutrient impacts on the Bay the Port Phillip Bay Phase I Study concluded that:

Taken as a whole, Port Phillip Bay, is . . . a relatively unpolluted body of water . . . Although nutrient concentrations are relatively high in the waters surrounding the sites of major inputs, extensive mixing in the immediate vicinity of the inputs diminishes concentrations rapidly.

Some nutrients occur at higher concentrations in the Bay than in Bass Strait, suggesting that a potential exists for high biological productivity in the Bay. Compared with polluted estuaries in various parts of the world, however, the abundance of plant and animal plankton (minute floating organisms) in the Bay is generally low.

A second phase of the Study (1975–1980) to some extent addressed questions raised by Phase I regarding the capacity of Port Phillip Bay to sustain waste loads from the urban and industrial growth of Melbourne. Work was undertaken to determine the local effects of the WTC discharges, but this work did not have the same level of integration as the Phase I Study, and the only overviews generated were by Axelrad et al. (1981) and Kelly et al. (1987).

Melbourne Water subsequently commissioned a review of the Phase II Study (Newell 1990) as part of a comprehensive appraisal of the effects of the WTC nutrient discharges on the ecology of the Bay. Newell concluded that

. . . the level of primary plant production in Port Phillip Bay is in equilibrium between ammonia input and a continual loss of DON (dissolved organic nitrogen). Most input nitrogen is therefore exported as DON to Bass Strait, although some DON may also be recycled.

Newell also stated that primary production is frequently controlled by light availability and mixing rates of Bay waters, rather than by nutrient availability. This finding is consistent with the conclusions of Axelrad et al. (1981).

Following the declaration of the SEPP for the Waters of Port Phillip Bay in 1975, a series of water quality monitoring programs were commissioned by the EPA. The results are reviewed by Longmore (1992) who concludes that the data do not enable the determination of changes in the nutrient status of the Bay over the last 15 years. This is despite a diversion of one-third of Melbourne's sewage to the South Eastern Treatment Complex in 1975. Over the three year period from 1975 to 1977 loads of nitrogen from the WTC were reduced by approximately 45%, from 6,200 tonnes of nitrogen per year to 3,500 tonnes per year. Unfortunately no specific studies were undertaken at the time to determine the impacts on the Bay of this substantial reduction in nutrient loads. Since 1977 loads have increased to approximately 4,000 tonnes of nitrogen per year (Fig. 3).

In 1987 a third phase of the Study was instigated, also with an emphasis on nutrients, but it languished after a period due to insufficient funding. The only projects completed were an investigation commissioned by Melbourne Water on the status of dissolved oxygen in the deep, central region of the Bay, undertaken by the Marine Science Laboratories (Mickelson 1990), and a review by MMBW of historical chlorophyll *a* data for the Bay (Brown 1989).
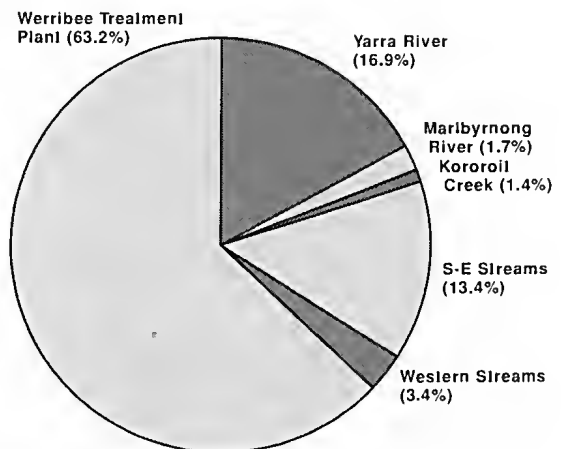

Fig. 3. Proportion of annual total nitrogen loads to Port Phillip Bay for 1980 from major surface inputs, including the Werribee Treatment Complex. Source: EPA Bulletins.

A proposal in 1990 by Melbourne Water to investigate the impact of nutrient loads from all sources on the western side of Port Phillip Bay was subsequently modified by an inter-agency technical committee (MMBW, EPA and the Victorian Department of Conservation and Environment) to address the entire Bay. A systems approach was proposed to provide a much improved understanding of the physical processes and nutrient dynamics, with the aim of developing a nutrients management plan for the Bay which would be effected as a schedule in the SEPP. The proposal failed to win management support, however, due to the perceived high costs involved.

In June 1991 the Minister for Conservation and Environment, Mr Steve Crabb, announced a major environmental study of Port Phillip Bay which is expected to set the agenda for environmental management of the Bay catchment for the next 20 years. The study will commence in June 1992 and will take 4 years to complete at a cost of up to $12 million. In July 1991 Melbourne Water, on behalf of the Study Management Committee (representing Melbourne Water, Department of Conservation and Environment, Environment Protection Authority and Port of Melbourne Authority), commissioned CSIRO to prepare a study design.

The management-based study objectives were evaluated to establish the scientific questions to be answered for both nutrient and toxicant issues. While recognizing that past and present work must be reviewed and integrated into the new research, scientific tasks have been defined which include a comprehensive understanding of the physical processes influencing transport, distribution and mixing of discharged materials; determination of nutrient and toxicant loads from inputs, their status in water and biota, and key transformation processes; and the role of sediments as storage reservoirs and as sites for transformation processes.

PLANNING FOR THE SUSTAINABLE DEVELOPMENT OF PORT PHILLIP BAY

While planning in Melbourne to date has been effective in minimising adverse environmental impacts on Port Phillip Bay, as Melbourne's size increases its supporting infrastructure must be augmented and improved to ensure that detrimental impacts are minimised.

The effects of present nutrient additions on the Bay remain largely unknown. Recent reviews of chlorophyll a data (a measure of phyto-plankton biomass) collected over the period 1969–1986 has shown that there have been statistically significant measurable increases in several of the segments but not over the entire Bay (Brown 1989, Saunders & Goudey 1990). In those segments where the increase is measurable it is not considered to be alarming (Brown 1989). Even so, concerns have been raised as to the present condition of Port Phillip Bay. Events that have been cited as causes for concern include the following.

(a) Local episodes of reduction in dissolved oxygen concentrations have been measured recently in the bottom waters of the Bay (Axelrad 1986, Mickelson 1990). It is not known whether the frequency and extent of these events are unusual for the Bay. Similar conditions have been raised as a cause for concern in comparable coastal systems elsewhere (Leffler 1990).

(b) Phytoplankton blooms are reported to have been observed as isolated occurrences although it is not documented as to where, when or how often. Phytoplankton blooms in coastal waters and embayments are very much a natural occurrence (Harris 1986), and quite high concentrations of chlorophyll a were reported during the extensive sampling program undertaken during the Phase I study (up to 20 mg/m^3).

(c) Blooms of toxic phytoplankton have been observed, particularly in the northern part of the Bay, and on at least one occasion associated with mortality of fish and shellfish (Arnott 1990). Although it is thought that blooms of these organisms are not a response to the input of nutrients from the WTC, they may nevertheless be important indicators of changing conditions in Port Phillip Bay.

(d) Reduction in seagrass density was measured during 1986 in the Geelong Arm, compared with measurements taken in 1981 (unpublished data, Marine Science Laboratories). While such reductions elsewhere have been shown to be a result of nutrient enrichment (Cambridge et al. 1986, Simpson et al. 1990), we do not know whether this is the case in Port Phillip Bay.

(e) Public concern persists over seaweed "washup" on metropolitan beaches. It has not been established whether seaweed biomass has increased over time in Port Phillip Bay, but if so it is important to establish the cause, and nutrient loads is one of the factors that would have to be considered.

Whether or not these matters are truly of concern and are a product of nutrient addition to the Bay, the problem remains that as the population

of Melbourne increases a point will be reached where the Bay will not be able to assimilate increased nutrient loads without major changes in ecosystem function and water quality. It is important that we determine in a scientific manner what are the acceptable loads, and that we build these into our strategic planning. This, in part, is the intention of the present study. The scientific information must, however, be considered in context with economic, social and engineering factors.

Provision of sewerage services to a large city like Melbourne requires long-term planning (up to 50 years) to ensure that the required capital works are put in place and that the very large costs (hundreds of millions of dollars) are spread over a number of generations. Cost estimates of four future development options for the WTC are listed in Table 1. A decision to upgrade the treatment facilities and to divert the discharge to Bass Strait (option 4) may result in an increase in the annual operating cost for the WTC of $145 million, $100 million of which would go to interest payments on the loans required to finance the capital works program. The cost to the community of some of these options represents not only an economic debt but also an opportunity cost, both in financial terms and in use of natural resources. That is, not only is the option lost to spend the money on other community needs such as education or health care, but the possibility also exists of imposing unnecessary

environmental impacts outside Port Phillip Bay.

It is therefore important that decisions on the provision of infrastructure to the city take into account all of the costs, options and consequences—environmental as well as economic and social. We believe the only successful way to ensure that this objective is met is through the development of a fully integrated waste disposal strategy for Melbourne, including a nutrient management plan for Port Phillip Bay and its catchment. This plan, which must be based on a sound scientific knowledge of the systems impacted, requires the integration of State policies and State environmental management initiatives with Melbourne Water's development strategies and with the implementation programs of other service agencies. Future plans by industry must also be considered.

ACKNOWLEDGEMENTS

System	Capital $M	Operating $M
Modified existing lagoon and land treatment system	120	20
Conventional primary treatment, improved lagoon and land treatment	260	35
Conventional primary and secondary treatment, improved lagoon and land treatment	480–540	40–45
Conventional primary and secondary treatment with ocean outfall	790–850	45

Table 1. Approximate capital and operating costs of major basic elements of future development options for the WTC. Factors such as interest and redemption capital borrowings are not included. Costs relate to predicted development with a dry weather flow of about 750 ML/day and are in 1987 $ values. Source: Stage 2 Summary Report, Werribee Treatment Complex Development Strategy, Board of Works, 1989.

REFERENCES

ARNOTT, G. H., 1990. *Surveillance of Toxic Marine Algae and Biotoxins in Shellfish in Port Phillip Bay.* Internal Report No. 187, Fisheries Division, Department of Conservation & Environment, Victoria.

AXELRAD, D. M., 1986. *Program PO5 Port Phillip Bay Eutrophication Project Research Proposal.* Program Review Series No. 60, Fisheries and Wildlife Service, Department of Conservation Forests and Lands, Victoria.

AXELRAD, D. M., POORE, G. C. B., ARNOTT, G. H., BAULD, J., BROWN, V., EDWARDS, R. R. C. & HICKMAN, N. J., 1981. The effects of treated sewage discharge on the biota of Port Phillip Bay, Victoria, Australia. In *Estuaries and Nutrients*, B. J. Neilson & L. E. Cronin, eds, Humana Press, Clifton, New Jersey, 279–308.

BREMNER, A. J. & CHIFFINGS, A. W., 1991. The Werribee Treatment Complex—an environmental perspective. *Water* 19 (3): 22–24.

BREMNER A. J., WOOD, K. & CHIFFINGS A. W., 1989. *Melbourne and the Coastal Environment: A*

Review of the Impact of Melbourne on Victoria's Coastal Environments. MMBW Environmental Studies Series No. 1/90, 58 p.

BROWN, V. B., 1989. *Long Term Trends in Chlorophyll "a" in Port Phillip Bay.* Environmental Services Series No. 89/001, Melbourne Board of Works, Victoria.

CARNOVALE, F. & SAUNDERS, J., 1988. *Appendum to the Deposition of Atmospheric Nitrogen Species to Port Phillip Bay.* SRS Report No. 87/002, Environment Protection Authority, Victoria.

CAMBRIDGE, M. L., 1975. Seagrasses of south-western Australia with special reference to the ecology of *Posidonia australis* Hook F. in a polluted environment. *Aquatic Botany* 1: 149–161.

CAMBRIDGE, M. L., CHIFFINGS, A. W., BRITTON, C., MOORE, E. & McCOMB, A. J., 1986. The loss of seagrass in Cockburn Sound, Western Australia, 2. Possible causes of seagrass decline. *Aquatic Botany* 24: 269–285.

CHIFFINGS, A. W. & McCOMB, A. J., 1981. Boundaries in phytoplankton populations. *Proceedings of the Ecological Society of Australia* 11: 27–38.

CROXFORD, A. H., 1978. Melbourne, Australia, wastewater system—case study. Paper presented at the 1978 winter meeting, American Society of Agricultural Engineers, Chicago, USA.

DINGLE, A. E. & RASMUSSEN, C., 1991. *Vital Connections: Melbourne and its Board of Works.* Penguin Books Australia, Ringwood, Victoria, 432 p.

GRANT, J. & SERLE, G. (eds), 1983. *The Melbourne Scene 1803–1956.* Hale & Iremonger, Sydney.

HARRIS, G. P., 1986. *Phytoplankton Ecology: Structure, Function and Fluctuations.* Chapman & Hall, London.

KELLY, R. A., POOLEY, G. J. & BREMNER, A. J., 1987. Port Phillip Regional Environmental Study Werribee Project, Task No. P01. Unpublished manuscript, Department of Conservation Forests and Lands, Victoria.

LEFFLER, M., 1990. Reading the hypoxia record: Clues below the bay bottom. Marine Notes: Maryland Sea Grant Publication Nov. 1–3.

LONGMORE, A., 1992. Nutrients in Port Phillip Bay: what has changed in 15 years? *Proceedings of the Royal Society of Victoria* 104: 00–00.

MANN, K. H., 1982. *Ecology of Coastal Waters. A Systems Approach.* Blackwell Scientific Publications, 322 p.

McPHERSON, J. B., 1979. Land treatment of waste water at Werribee past, present and future. *Progress in Water Technology* 11 (4/5): 1–17.

MACPHERSON, J. H. & LYNCH, D. D., 1966. Port Phillip Survey 1957–1963. Introduction. *Memoirs of the National Museum of Victoria* 27: 1–5.

MICKELSON, M. J., 1990. *Dissolved Oxygen in Bottom Waters of Port Phillip Bay.* Environmental Services Series No. 90/010, Melbourne Board of Works.

MMBW, 1990a. *Annual Report of the Melbourne Board of Works.* Melbourne Board of Works, Melbourne, Victoria.

MMBW, 1990b. *Proposed Programme of Investigations Including the Port Phillip Bay Study—Phase III.* Environmental Services Series No. 90/001, Melbourne Board of Works.

MMBW/FWD, 1973. *Environmental Study of Port Phillip Bay: Report on Phase One 1968–1971.* Melbourne and Metropolitan Board of Works & Fisheries and Wildlife Department of Victoria.

NEWELL, B. S., 1990. *An Appraisal of the Effects of the Werribee Treatment Complex Discharge on the Ecology of Port Phillip Bay.* Environmental Services Series No. 90/007, Melbourne Board of Works, Victoria.

ROCHFORD, D. J., 1966. Port Phillip Survey 1957–1963. Hydrology. *Memoirs of the National Museum of Victoria* 27: 107–118.

SAUNDERS, J. & GOUDEY, R., 1990. *Trends in Chlorophyll-a Data, 1970–86.* SRS Report No. 90/013, Environment Protection Authority, Victoria.

SEEGER, R. C., 1961. The history of Melbourne's sewerage system. Unpublished manuscript, Melbourne Water, Victoria.

SILBERSTEIN, K., CHIFFINGS, A. W. & McCOMB, A. J., 1986. The loss of seagrass in Cockburn Sound, Western Australia, 3. The effects of epiphytes on productivity of *Posidonia australis* Hook. F. *Aquatic Botany* 24: 355–371.

SIMPSON C. J., BOTT, G., GEORGE, R., LUKATELICH, R. J. & PARKER, I., 1990. *Albany Harbours Environmental Study (1988–1989). A report to the Environmental Protection Authority from the Technical Advisory Group.* EPA Bulletin 412. Perth, Western Australia.

APPENDIX

A number of estimates of nutrient loads from the WTC to Port Phillip Bay have been made over the last 20 years. A brief description of how these estimates were derived is given below.

1. *PPB Environmental Study, Phase I, 1973.* The loads calculated during this study are based on monthly grab samples of effluent analysed for nutrient concentrations, and outflow rates for WTC discharge drains estimated by WTC personnel calibrated to measurements by a Gurley propeller-type current meter. The period of measurements was from 1968–1971.

2. *Western Environmental Study, 1977.* (D. Lynch, P. Scott & J. Constable, unpublished report, Melbourne Water. Loads were calculated using influent sewage volumes and nutrient concentrations, and estimated loading removal rates of WTC treatment processes. This was done for the periods 1969/70, 1973/4, 1979/80, 1980/81, 1984/85, 1985/86.

3. *WTC ("Farm") estimates, 1984.* Loads were calculated using weekly grab samples of effluent analysed

for nutrient concentrations, and outflow rates adjusted to 1983/84 percentage inflows processed through to particular outlets. There is some doubt about 1983/84 outflow measurements.

4. *WTC ("Farm") estimates, 1986 >*. Loads were calculated using monthly grab samples of effluent (1973/74–1975/76) and weekly grab samples (1976/77–1981/2) analysed for nutrient concentrations, and outflow rates adjusted to 1984/85–1985/86 percentage inflows processed through to particular outlets. The 1984/85 and 1985/86 loads are based on continuous flow monitoring at each outlet and weekly grab samples of effluent analysed for nutrient concentrations at all five EPA licensed outlets.

5. *J. Constable (2 year), 1987*. Loads were calculated by estimating the N discharge rate to the Bay as the difference between the nitrogen mass load delivered to the WTC annually and the estimated nitrogen removal rates of the different treatment processes. A two year average of monthly sampled total N concentrations of 58 mg/L for influent was used. The two year period used is not documented.

6. *J. Constable (10 year), 1987*. Loads were calculated by estimating the N discharge rate to the Bay as the difference between the nitrogen mass load delivered to the WTC annually and the estimated nitrogen removal rates of the different treatment processes. A ten year average of monthly sampled total N concentrations of 62 mg/L for influent was used. The ten year period used is not documented.

NUTRIENTS IN PORT PHILLIP BAY: WHAT HAS CHANGED IN 15 YEARS?

Andrew Longmore

Marine Science Laboratories, Department of Conservation and Environment, PO Box 114, Queenscliff, Victoria 3225

Various aspects of the nutrient status of Port Phillip Bay have been studied over the past 15 years by government agencies including the Environment Protection Authority (EPA) and the Marine Science Laboratories (MSL). The results of these studies, each of which had different objectives, are summarised in this paper. Partly because sampling design varied with each study, it is not possible to detect significant changes in the nutrient status of the Bay during the past 15 years.

PORT PHILLIP Bay is a shallow basin with a mean depth of 14 m and a maximum depth of 22 m. Nearly 350 point sources discharge to the Bay, with the Yarra/Maribyrnong and Werribee river systems being the largest freshwater sources (MMBW/FWD 1973). Annual evaporation approximates annual streamflow (about 5% of mean Bay volume) and, except near discharges, salinity is close to oceanic levels. In Corio Bay, where evaporation exceeds freshwater inflow, water is often hypersaline.

For many years, concern has been expressed about: (1) the potential for the Bay to become eutrophic as a consequence of excessive addition of nutrients; and (2) the effect which eutrophication may have on beneficial uses of the Bay (MMBW/FWD 1973). Such concerns have determined the direction of all nutrient studies.

In this paper the results of monitoring programs carried out by the EPA and MSL over the past 15 years (1975–1977, 1980–1984, 1985–1986 and 1985–present) are summarized, and suggestions are made on ways to obtain the information needed for a comprehensive understanding of the effect of nutrients on the Bay ecosystems.

EPA 1975–1977

The State Environment Protection Policy (SEPP) for waters of Port Phillip Bay, declared in 1975, defined water quality standards for the Bay and set objectives against which water quality could be measured. Beneficial uses (such as aesthetic enjoyment, maintenance and preservation of natural aquatic ecosystems, production of fish) were to be protected by the licensing of point source discharges and monitoring of the Bay waters. However, licence conditions are set without knowledge of the effects of the discharge in the discharge zone.

In the SEPP the Bay was divided into nine segments (Kowarsky 1992, fig. 1) on the basis of nutrient concentrations determined in the first major study (1969–1970, MMBW/FWD 1973). A grid of potential sampling sites was designed for each segment, and water was sampled from near-surface, mid-water and bottom water depths at four randomly selected sites within each of the segments at about six-weekly intervals during October 1975–March 1977. Many of the potential sites were not sampled, while some were sampled more than once. Each sample was analysed by MSL for salinity, temperature, dissolved oxygen, pH, suspended solids, nitrate, nitrite, ammonium, total phosphorus, reactive phosphorus and phytoplankton pigments.

Variations in nutrient and chlorophyll concentrations with water depth were minimal, except for samples from the Werribee segment where highest concentrations occurred near the surface (EPA 1979). Nutrient concentrations varied so much within segments that no regions of homogeneous water quality were found in any segment. The highest variability was in those segments (Werribee, Hobsons Bay) with the largest fresh water discharges. These were also the segments with the highest mean nutrient concentrations.

A statistical analysis of the concentrations of three water quality indicators (ammonium, nitrate and total phosphorus) showed that variance within segments was often higher than variance between sampling times (Table 5.5 in EPA 1979). Random stratified sampling is not

the most appropriate sampling regime for detecting trends in time (though that was not the objective of the program). When compared with the SEPP objectives, compliance for total phosphorus and chlorophyll *a* was poor in almost all segments; the cruise mean average compliance was 68% for total phosphorus and 41% for chlorophyll *a*. Compliance for other indicators (dissolved oxygen, pH, water clarity) was generally good.

EPA 1980–1984

The second water quality monitoring program carried out by EPA was again concerned with compliance of water quality indicators with the SEPP objectives; surface waters only were sampled. During June 1980–May 1982 samples were collected monthly from a site selected randomly from within each of 16 strata (Fig. 1). The majority of the strata (11 out of 16) were located in the north and western one-third of the Bay;

the data averages from this study are therefore biased toward the more industrialized areas of the Bay.

Total organic carbon, Kjeldahl nitrogen and silicate concentrations were also determined.

The results in summary are as follows.
(1) Compliance with the SEPP objectives for chlorophyll *a* was better in all segments than it had been in the 1975–1977 study.
(2) In the Exchange segment, which has a more stringent chlorophyll objective than other segments, only 50% of observations met the objective.
(3) Average compliance for dissolved oxygen in surface waters was lower in 1980–1982 than in 1975–1976 (67% compared with 84%).
(4) Inorganic nitrogen 90th percentile concentrations were higher in the Yarra mouth during 1980–1982 than during 1975–1976, while total phosphorus 50th concentrations were higher in all strata during 1980–1982.
(5) Average compliance for total nitrogen was greater than 95%.
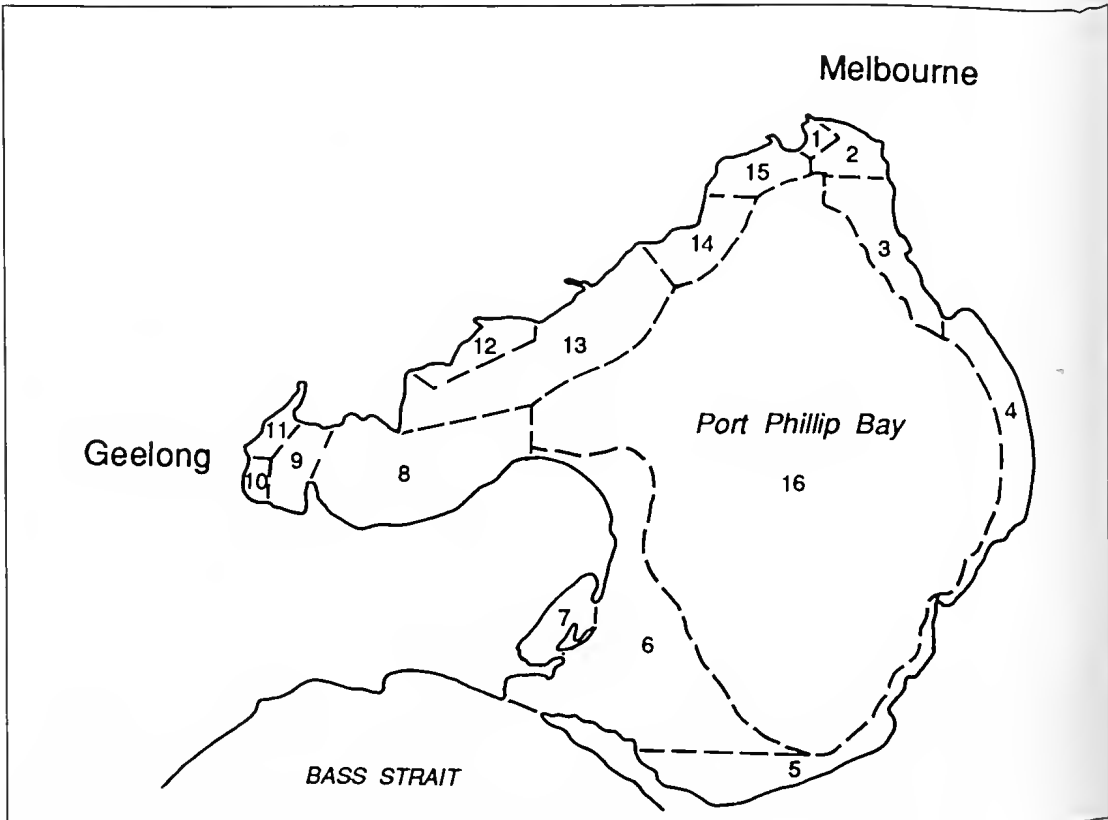
Fig. 1. Strata of Port Phillip Bay sampled during 1980–1986.

Sampling continued during October 1982–June 1984 in the same format as for 1980–1982 and the analytical results of all 48 cruises (1980–1984) have been summarized (Cowdell et al. 1985).

During 1980–1984, highest mean reactive phosphate and inorganic nitrogen concentrations occurred in stratum 12 (Werribee Farm), while mean chlorophyll *a* concentrations were highest in strata 1 and 2 (Hobsons Bay; 2.6–2.7 µg L⁻¹). Chlorophyll *a* concentrations were lowest in strata 5 and 6 (South-Eastern and Exchange; 0.7 µg L⁻¹), while strata 12 and 13 (Werribee segment) were intermediate in concentration (2.2–1.2 µg L⁻¹). There was no direct correlation between areas of high nutrient concentration and areas of high chlorophyll concentration. Mean Secchi disc depth was low in the Yarra mouth and Hobsons Bay (strata with highest mean chlorophyll *a* concentrations), suggesting that turbidity did not limit phytoplankton growth during 1980–1984. This contradicts the argument advanced by the EPA (EPA 1983) that increased runoff during 1980–1982 led to greater turbidity in the Bay, limiting phytoplankton growth. Conversely, mean chlorophyll concentrations were too low (less than 10 µg L⁻¹) to make a significant contribution to light attenuation (Kirk 1976); low Secchi disc depths indicated high inorganic particulate loads.

When a volume-weighted correction is made to compensate for most of the measurements being made in relatively shallow near-coastal waters, baywide annual mean chlorophyll *a* concentrations increased significantly (by analysis of variance with multiple t-tests at the 5% significance level) from 1980/81 to 1981/82, and from 1982/83 to 1983/84, with a statistically non-significant decrease from 1981/82 to 1982/83. The mean chlorophyll *a* concentration over the period was 0.79 µg L⁻¹.

EPA/MSL 1985–1986

During July 1985–June 1986, water quality data for Port Phillip Bay were obtained from quarterly sampling at 28 fixed sites throughout the Bay; from monthly sampling at 4 sites in the Central segment; from hourly sampling for one 24-hour period in Corio Bay in July 1975 and January 1976; and from on-board analysis of water collected continuously during 4 cruises (August and November 1985; February and May 1986) along transects across the Bay (Longmore et al. 1990). As well as collecting samples

for comparison with the SEPP objectives for Port Phillip Bay, the objectives of this study were:
(1) to determine spatial and temporal trends in water quality; and (2) to determine, through studies of effluent plumes, the extent and pattern of influence of major inputs of river water or effluents on water quality.

Spatial and temporal trends

Total phosphorus concentrations at the 28 fixed sites varied little over the year, except off the Werribee Treatment Complex (WTC) where concentrations were highest in winter. Similarly, ammonium and nitrate concentrations were highest off the WTC in winter and very low in summer. The Yarra River discharged inorganic nitrogen throughout the year, and the Werribee River was an important source of nitrate during winter. Chlorophyll *a* concentrations were generally twice as high during the winter months, and were highest off Werribee in winter–spring.

Plumes

The extent and pattern of influence of major inputs of fresh water and effluents on water quality of the Bay is not well known. The program was designed to provide information on the influence of inputs from the Yarra River, Werribee River, WTC, sources in Corio Bay and the Patterson River.

Continuous on-board analysis showed that the Yarra River created a larger fresh water plume than the Werribee and Patterson rivers and the WTC. The Yarra River plume affected salinity predominantly on the eastern side of the Bay. During August 1985 the plumes of fresh water from the Yarra River, Werribee River and the WTC clearly affected the salinity of at least half of the surface waters of Port Phillip Bay (Fig. 2).

Phosphate discharge from the Yarra River was evident on all cruises but its effect was not observed much beyond Hobsons Bay. The input of phosphate from the WTC exceeded all other point discharges during autumn and winter, and affected the western one-third of the Bay.

Nitrate plumes were negligible during summer but were detectable off the WTC in spring and autumn, off Werribee River in winter, and in Hobsons Bay on all cruises.

Highest chlorophyll concentrations were observed off WTC in winter, spring and autumn.
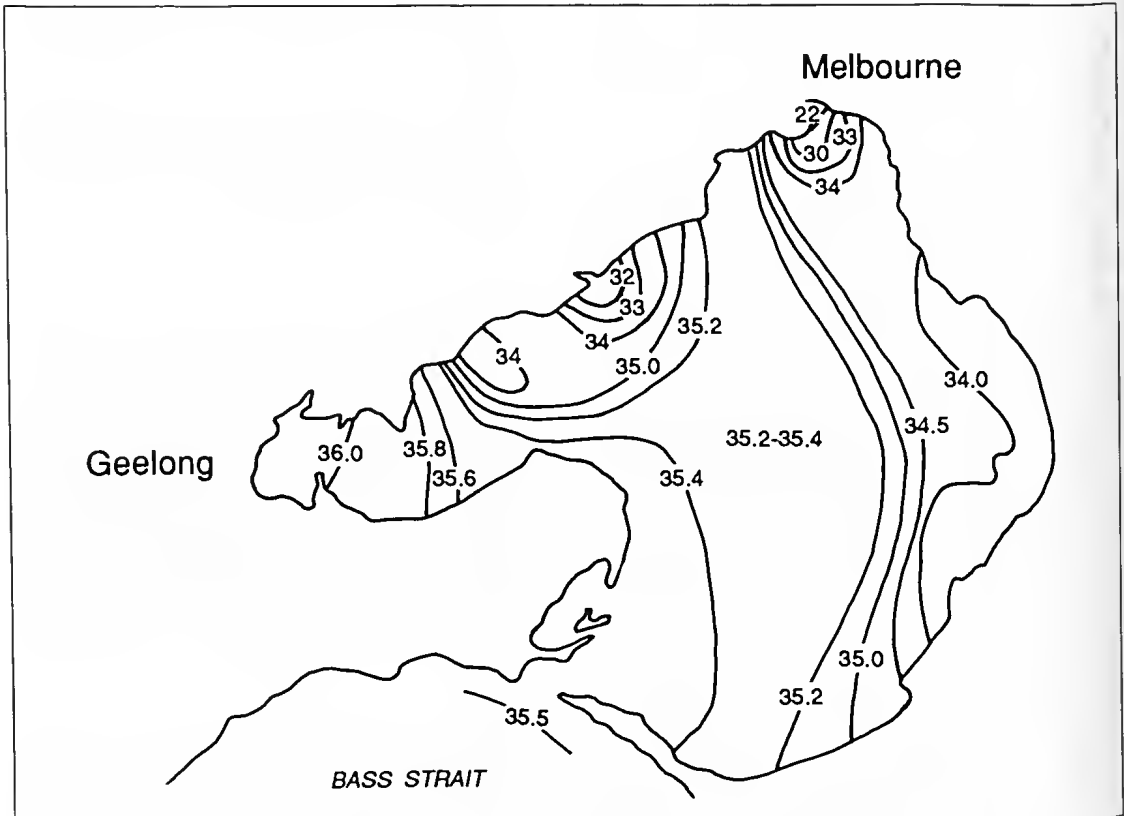
Overall compliance of the water quality data

Fig. 2. Effect of fresh water discharge on surface salinity of Port Phillip Bay during August 1985.

with SEPP objectives was similar to the compliance in 1980–1982; compliance for concentrations of total phosphorus and chlorophyll *a* in water samples from all segments of the Bay was poor. In winter, no sample from any segment met the chlorophyll objective. Typical chlorophyll concentrations were 2–6 times the objective.

LOOKING FOR TRENDS

Given that the SEPP objectives were drawn from the mean concentrations of nutrients found during the 1969–1970 study, it is important to explain why in all studies since 1975 chlorophyll and total phosphorus concentrations have failed to meet the objectives. Was 1969–1970 a period of low nutrient concentrations and low plankton production, or have concentrations increased since then? Can we be certain that the differences in nutrient and chlorophyll concentrations observed in the Bay since 1969 are not due to different analysts

and/or different methods? In a summary of the data collected to date from the central segment of the Bay (which contains 57% of the surface area and 80% of the volume of the Bay, and is the only segment to have been sampled in all studies listed here), it is difficult to distinguish a trend in either chlorophyll *a* or inorganic nutrient median concentration with time (Table 1). We could conclude that, at least in the centre of Port Phillip Bay, there is no evidence for concern about the effects of current nutrient discharges. Shallower waters close to coastal discharges have not been studied over the same period of time, and the effect of nutrients on productivity close to the Bay shore is not yet understood.

Because of the discontinuous nature of the data gathered before 1984 it was not possible to apply time series analytical techniques to determine statistically significant temporal trends. However, Saunders & Goudey (1990) pooled chlorophyll *a* concentrations by stratum and showed that the data gathered from segments of the Bay are not normally distributed. Using a

Study	PO_4	NH_4	NO_{2+3}	SiO_4	Chl$a$	Salin.	Temp.
1969–1970 (1)	2.1	3.6	0.6	0.5	1.2	34–37.4	11–22
1975–1976 (2)	1.7	0.4	0.1	—	1.1	—	—
1975–1977 (3)	1.9	0.5	0.3	—	1.5	31.1–37.4	10–22
1980–1984 (4)	1.9	0.2	0.1	3.7	0.8	31.2–38.8	8.5–23
1985–1986 (5)	1.9	<0.1	<0.1	1–11	1.2	34.8–35.7	10–21
1987–1989 (6)	2.0	0.5	0.1	7.0	1.1	34.3–35.7	10.3–21

Table 1. Comparison of results from the central segment of Port Phillip Bay. Median nutrient concentrations in μM, chlorophyll a in μg L^{-1}, temperature in °C. Study key: (1) = Phase I, MMBW/FWD (1973); (2) = Axelrad (1978); (3) = EPA (1979); (4) = Cowdell et al. (1985); (5) = Longmore et al. (1990); (6) = Mickelson (1990). Note that median ammonium (NH_4) and oxidized nitrogen (NO_{2+3}) concentrations reported in Phase I were far higher than those measured since, and salinity and temperature extremes have varied from study to study but not necessarily from year to year. Random site selection and inadequate sampling frequency means extremes may have been missed.

non-parametric seasonal Kendall test, a statistically significant decline in chlorophyll a concentration was observed during 1975–1986 in the Corio Urban stratum, and significant increases in chlorophyll concentration were detected in the Werribee Farm and Altona strata. This analysis assumes that: (1) the effect of variation due to location within a segment (or stratum) can be neglected if sufficient random samples are collected within each segment; and (2) the sampling intensity and variance within each segment is the same over time. A more robust analysis could be made if variation due to location could be ruled out completely by sampling at geographically fixed sites.

EPA FIXED SITES 1984–PRESENT

In 1984 EPA began regular (2–4 weekly) monitoring at three fixed sites in the Bay: Hobsons Bay, Corio Bay and central Port Phillip Bay. A recent analysis of the data (D. Robinson, pers. comm.) using a Kendall test of association found that there were increasing trends in most indicators monitored. During 1984–1989 significant increases in total phosphorus concentrations occurred only at the Bay centre and Corio Bay sites. There were no statistically significant changes in chlorophyll a, dissolved oxygen, phosphate or inorganic nitrogen concentrations. Upward (non-significant) trends were observed in total nitrogen concentrations.

The same analysis could not be extended to data gathered before 1984, since all previous sampling programs were based on random sampling within each segment, introducing variation due to location within the segment.

It is reasonable to ask whether the total nutrient input to the Bay (as distinct from nutrient concentrations in the Bay) has increased during the past 15 years. Estimates by Melbourne Water of nitrogen and phosphorus loads from the WTC to the Bay suggest that loads have increased by less than 15% since 1975. EPA fixed site river sampling, particularly in the Yarra River, indicated the same general increasing nutrient concentration trend during 1984–1989 as was observed for the fixed sites in the Bay (that is, an increasing trend in nitrogen and phosphorus concentrations in most rivers entering the Bay, but the only significant trend was for total phosphorus). However, neither of these studies have taken into account the effect of storm events, during which a large proportion of annual nutrient load may be transported. Work is proceeding to determine the current influence of storm events in streams and the WTC, but the following questions remain. Can load estimates be corrected for past storm events? Are past estimates of nutrient load meaningful?

Following intensive connection of unsewered residential areas of Melbourne to the sewer during the 1970s and EPA licensing of industrial discharges, the water quality of Port Phillip Bay was expected to improve; there is no firm evidence that this has happened.

FUTURE DIRECTIONS

To understand better the effects of nutrient inputs on the Bay, the following is needed:
(1) a more complete data set (both from nutrient inputs and from Bay waters) to determine *long-term trends*;
(2) an accurate measure of the *areas of the Bay impacted most* by nutrient inputs;
(3) cheaper *sampling strategies*;
(4) better understanding of nutrient cycling

between water, sediments and biota of the Bay;

(5) *better indicators* of water quality, with emphasis on an early warning of trends toward eutrophication.

Long-term trends

MSL is responsible for the management of the estuarine and marine fisheries of Victoria. A monitoring program of fixed sites was recently commenced by MSL to determine nutritional and physicochemical factors which affect the food chain in Port Phillip Bay at its lowest level (plankton). Regular water sampling in six areas of high fishing pressure in Port Phillip Bay will permit the use of time series analytical procedures for examining long-term trends in ambient water quality. This work will thereby complement the EPA Fixed Sites program. With some further work to define the effect of flood events, the EPA river monitoring program and monitoring of the Werribee Treatment Complex by Melbourne Water should allow us to determine trends in inputs to the Bay.

Areas impacted most

When plankton die they settle to the bottom of the Bay and decay, producing a sediment oxygen demand (SOD). Increasing nutrient supply which leads to increased algal biomass should be reflected in an increased SOD. If waters are stratified, SOD may cause decreases in oxygen concentration (hypoxia) below the pycnocline, which in extreme cases could have catastrophic effects on, for example, scallop spat (Body & Murai 1986). While recent Melbourne Water/ MSL work showed that water in central Port Phillip Bay is rarely hypoxic (Mickelson 1990), no measurements of SOD had been made elsewhere in the Bay. A bay-wide survey of SOD carried out in 1991 will, when analysed, assist in identifying those areas of the Bay currently impacted most by nutrient inputs and the possibility of their being affected by hypoxia.

Sampling strategies

Sampling of Bay waters from boats and subsequent chemical analysis is expensive. Sentinel organisms have been used for estimating the cumulative effect of heavy metals and hydrocarbons on the biota of the Bay. However, indicator organisms are not used for nutrients; all nutrient sampling programs to date have involved water analyses only. Effort could be

directed into identifying possible indicator organisms (e.g. macroalgal biomass) or techniques (e.g. fouling plates), saving both time and effort. Sediments may also act as integrators of nutrient input, through their role in the storage and recycling of organic matter which settles to the bottom, and it may be possible to use infrequent sediment surveys to monitor long term trends in organic supply or oxygen demand, or to detect biomarkers in sediment.

Better indicators

Are water quality indicators sufficient to achieve the SEPP objectives? Fourteen years ago, Axelrad (1978) demonstrated nitrogen limitation in nutrient enrichment bioassays of phytoplankton from Port Phillip Bay. Phytoplankton require about 15 atoms of nitrogen for each atom of phosphorus and preferentially absorb inorganic nutrients. The mean atomic ratio of inorganic nitrogen to inorganic phosphorus in Port Phillip Bay is about 1:5, emphasising the probability of nitrogen limitation. During all of the surveys taken so far, chlorophyll concentrations in Port Phillip Bay have exceeded the SEPP objectives; on the other hand, total nitrogen concentrations were below the SEPP objectives. If this indicates excessive phytoplankton growth in Port Phillip Bay, and if phytoplankton growth in the Bay is nutrient-limited, then it follows that the SEPP nutrient objectives are too high to prevent excessive algal growth.

There are only two nutrient indicators in the SEPP: total nitrogen and total phosphorus. Over most of the Bay the SEPP for total nitrogen is irrelevant to growth of plankton because more than 90% of the dissolved nitrogen in many segments of Port Phillip Bay is in refractory organic forms unavailable to plankton. However, nutrients in sewage discharges (e.g. from Werribee) are predominantly in inorganic (readily available) forms, and the SEPP for total nitrogen may have some relevance in areas affected by such discharges.

An SEPP for inorganic nitrogen may appear to be more relevant to growth of plankton, but uptake of inorganic nitrogen is rapid close to discharges, and ambient concentrations for the whole Bay do not reflect the input rate or its effect.

It could be argued that, in a nitrogen-limited system without significant N_2 fixers, phosphate is in excess and higher phosphate concentrations are unlikely to cause more algal blooms. Inorganic nitrogen is rapidly taken up by both phyto-

plankton and benthic plankton, particularly near Werribee (Axelrad et al. 1979); thus increasing phosphorus concentrations over time could be interpreted as the result of an increased discharge of both inorganic nitrogen and phosphorus, with the inorganic nitrogen having been utilized close to the discharge.

Relying on chlorophyll *a* as an indicator may not be satisfactory, particularly on a local scale. For example, Axelrad et al. (1979) estimated that benthic productivity near Werribee was 3–5 times that of plankton in the water column. Effects of nutrient inputs from the WTC may be more easily observed in the benthos than in the phytoplankton.

If management objectives are to keep phytoplankton growth to the SEPP objectives, there needs to be a strategic review. Simultaneously, the quantitative relationships between fish populations and "excess" phytoplankton growth should be determined for the Bay. One of the beneficial uses to be protected is the maintenance and preservation of natural aquatic ecosystems and wildlife; maintaining a particular chlorophyll *a* concentration may not be enough to protect that beneficial use. It is also important to realise that low numbers of toxic phytoplankton may be sufficient to cause enormous problems, without affecting the total chlorophyll *a* concentration. Perhaps the best way to monitor phytoplankton in Port Phillip Bay is by regular counting of each species; MSL is currently doing that.

ACKNOWLEDGEMENTS

REFERENCES

Axelrad, D. M., 1978. *Effect of the Werribee Sewage Treatment Farm Discharge on Phytoplankton Productivity, Biomass and Nutrients in Port Phillip Bay*. Environmental Study Series No. 170, Ministry for Conservation, Victoria.

Axelrad, D. M., Hickman, N. J. & Gibbs, C. F., 1979. *Microalgal Productivity as Affected by Treated Sewage Discharge to Port Phillip Bay*. Environmental Study Series No. 241, Ministry for Conservation, Victoria.

Body, A. G. C. & Murai, T., 1986. Scallop culture in Japan. *Australian Fisheries* 45(9): 30–32.

Cowdell, R. A., Gibbs, C. F., Longmore, A. R. & Theodoropoulos, T., 1985. Tabulation of Port Phillip Bay water quality between June 1980 and July 1984. Marine Science Laboratories Internal Report No. 98, Marine Science Laboratories, Queenscliff.

EPA (Environment Protection Authority, Victoria), 1979. *Port Phillip Bay Water Quality Monitoring Program, October 1975–March 1977*. Report No. 93/79, Melbourne.

EPA (Environment Protection Authority, Victoria), 1983. *Port Phillip Bay Water Quality, June 1980–May 1982*. Environment Protection Authority Publication No. 181, Melbourne.

Kirk, J. T. O., 1976. Spectral absorption properties of natural waters: contribution of the soluble and particulate fractions to light absorption in some inland waters of south-eastern Australia. *Australian Journal of Marine and Freshwater Research* 31: 287–296.

Kowarsky, J., 1992. Aquaculture and nutrients—developing policies for protecting the environment of Port Phillip Bay. *Proceedings of the Royal Society of Victoria* 104: 00–00.

Longmore, A. R., Cowdell, R. A. & Gibbs, C. F., 1990. *Monitoring of Water Quality in Port Phillip Bay, 1985–86*. Scientific Report Series No. 89/003, Environment Protection Authority, Victoria.

MMBW/FWD, 1973. *Environmental Study of Port Phillip Bay. Report on Phase I, 1968–1971*. Melbourne and Metropolitan Board of Works & Fisheries and Wildlife Department of Victoria.

Mickelson, M. J., 1990. *Dissolved Oxygen in Bottom Waters of Port Phillip Bay*. Environmental Services Series No. 90/010, Melbourne and Metropolitan Board of Works, Victoria.

Saunders, J. & Goudey, R., 1990. *Trends in Port Phillip Bay Chlorophyll-a Data, 1970–86*. Scientific Report Series No. 90/013, Environment Protection Authority, Victoria.

AQUACULTURE AND NUTRIENTS—DEVELOPING POLICIES FOR PROTECTING THE ENVIRONMENT OF PORT PHILLIP BAY

John Kowarsky

Strategic Policy Branch, Policy Division, Environment Protection Authority, 477 Collins Street, Melbourne, Victoria 3000

Interrelationships between aquaculture and nutrients in Port Phillip Bay are explored in the context of the State Environment Protection Policy (The Waters of Port Phillip Bay). Approaches to protecting the beneficial use "production of edible shellfish without the addition of nutrients" from adverse effects of nutrient enrichment are discussed. It is concluded that a monitoring program for the early detection of algal blooms is essential to protect both public health and the aquaculture industry.

THROUGH its Aquaculture Initiative, the Victorian Government signalled its intention to facilitate the development of commercial aquaculture ventures (Victorian Government 1987a). Marine aquaculture, or mariculture, is of topical interest as a relatively new and expanding use of water in this State, and Port Phillip Bay is at present the site of almost all of Victoria's commercial mariculture. Nutrients are of great significance to the success of any aquaculture operation.

As the State Environment Protection Policy (SEPP) (The Waters of Port Phillip Bay) is at present under review, this is an opportune time to discuss some of the policy issues relating to the management of aquaculture within the Bay. In a more general sense, a discussion of the interrelation of the three subjects in the title of this paper should illustrate the Victorian Government approach to "protecting" Port Phillip Bay from pollution.

Before discussing how aquaculture and nutrients interrelate within the Bay, it is necessary to provide some background as to the way in which environmental policies have developed in Victoria.

THE CONCEPT OF BENEFICIAL USES

A "beneficial use" has been defined as "a use of the environment or any element or segment of the environment that is conducive to public benefit, welfare, safety, or health and which requires protection from the effects of waste discharges, emissions and deposits" (Section 4(1) of the Environment Protection Act 1970; Victorian Government 1987b). Examples of beneficial uses of water include (EPA 1983):

(a) potable water supply;
(b) agricultural water supply;
(c) industrial water supply;
(d) hydro-electric power generation
(e) navigation and shipping;
(f) recreation;
(g) production of edible fish and crustaceans;
(h) shellfish culture and harvesting;
(i) maintenance of aquatic ecosystems;
(j) maintenance of modified aquatic ecosystems;
(k) maintenance of water-associated wildlife;
(l) recharging of aquifers; and
(m) scientific and educational uses.

Under the above definition, use of the environment as a sink for discharge of wastes is clearly not a beneficial use.

Not all beneficial uses will apply to any given body of water, and some uses may exclude others; for example, use of water for a shipping channel may preclude its use for recreation.

Some beneficial uses may have the potential to lead to environmental degradation. For example, recreational boating activities may, in the extreme, lead to contamination of water by motor fuel, fumes, anti-foulants and human wastes. In general, however, the deleterious environmental effects of beneficial uses are relatively minor and short-term.

Each beneficial use of water has a suite of environmental indicators considered relevant for its protection. For example, the bacterial concentration of water is a relevant indicator for the beneficial use "swimming" but not for "industrial cooling". Each relevant indicator is given a level (an "objective") to be maintained or achieved to protect the beneficial use being considered. The objective is based upon published

standards and research results. An attainment program outlines the mechanism by which environmental goals are to be achieved.

Deciding upon the beneficial uses of a given segment of the environment requires an assessment and balancing of the present status and use of that segment, its potential future use, and whatever environmental improvements can be realistically attained. Once an SEPP is declared, the Victorian Government is committed to protecting the defined beneficial uses against adverse effects of pollution.

SEPPs are policies of the Victorian Government and must be complied with by all organisations, including government bodies, and individuals.

THE STATE ENVIRONMENT PROTECTION POLICY—THE WATERS OF PORT PHILLIP BAY

This policy was declared in 1975. Port Phillip Bay is divided into nine segments (Fig. 1) and beneficial uses of the water of each segment are listed.

Aquaculture is not specifically listed as a beneficial use but would fall in one of the following two.

1. Production of fish and crustaceans for human consumption. This use is protected in all segments of the Bay except the Werribee segment.

2. Production of fish, crustaceans and shellfish for human consumption. This is a protected beneficial use only in the Exchange and Central segments of Port Phillip Bay. "Shellfish" is undefined but in this context could be taken to include bivalve and probably other mollusc groups.

For each of the segments the Policy gives the same general objective for the indicator "nutrients and biostimulants"; i.e. "Waste discharges shall not add nutrient substances or other growth stimulants in quantities sufficient to cause excessive or nuisance algal or other plant growth...". In addition, numerical objectives for total nitrogen, total phosphorus and chlorophyll *a* levels are specified and differ between segments.

In the recommended water quality criteria manual (EPA 1983), "nutrients" was not considered a relevant water quality indicator for the beneficial uses "shellfish culture and harvesting" or "production of edible fish and crustacea". This is an error, as biological phenomena related to nutrients in the water can profoundly

affect aquaculture organisms and their human consumers.

Another SEPP, the SEPP (Waters of Victoria), declared in 1988, applies to all surface waters of Victoria except where varied by any SEPP separately declared.

TYPES OF AQUACULTURE

Aquaculture can be divided broadly into two categories.

1. *Active-feeding aquaculture.* The cultured organisms are provided with food, such as pellets or trash fish (e.g. caged salmon culture), or the environment is enriched by the application of fertilisers to provide for greater primary production (e.g. some pond culture of fish and crustaceans).

2. *Passive-feeding aquaculture.* The organisms rely wholly on naturally occurring food, usually by filter-feeding on phytoplankton (e.g. mussel farming). No food is provided directly or by the addition of inorganic nutrients to stimulate primary production.

ENVIRONMENTAL EFFECTS OF AQUACULTURE

A comparison of the environmental effects of active- and passive-feeding aquaculture with regard to nutrients has been made by Gowen et al. (1988), Folke & Kautsky (1989) and Woodward (1989).

The nitrogen budgets of a salmon cage farm and a mussel long-line farm are very similar; in both cases about 75% of the nitrogen in the food supply forms either solid or soluble waste (Folke & Kautsky 1989). The fundamental difference between the two is that in the case of the salmon farm the food supply is added, and there is a potential for hypernutrification which in turn may lead to eutrophication (Gowen et al. 1988). By contrast, there is evidence that mussel farming may lead to nutrient reduction (Kaspar et al. 1985).

It is possible to gauge the extent to which salmon and mussel farming activities may affect the nitrogen budget of a waterbody. For the purpose of this exercise assume that for each species an annual crop of 500 tonnes net weight of product is harvested. In the case of salmon, this is approximately equivalent to 12.8 tonnes nitrogen (assuming that 16% of wet weight is protein and that 16% of protein is nitrogen). From the relationship given in the previous paragraph, it
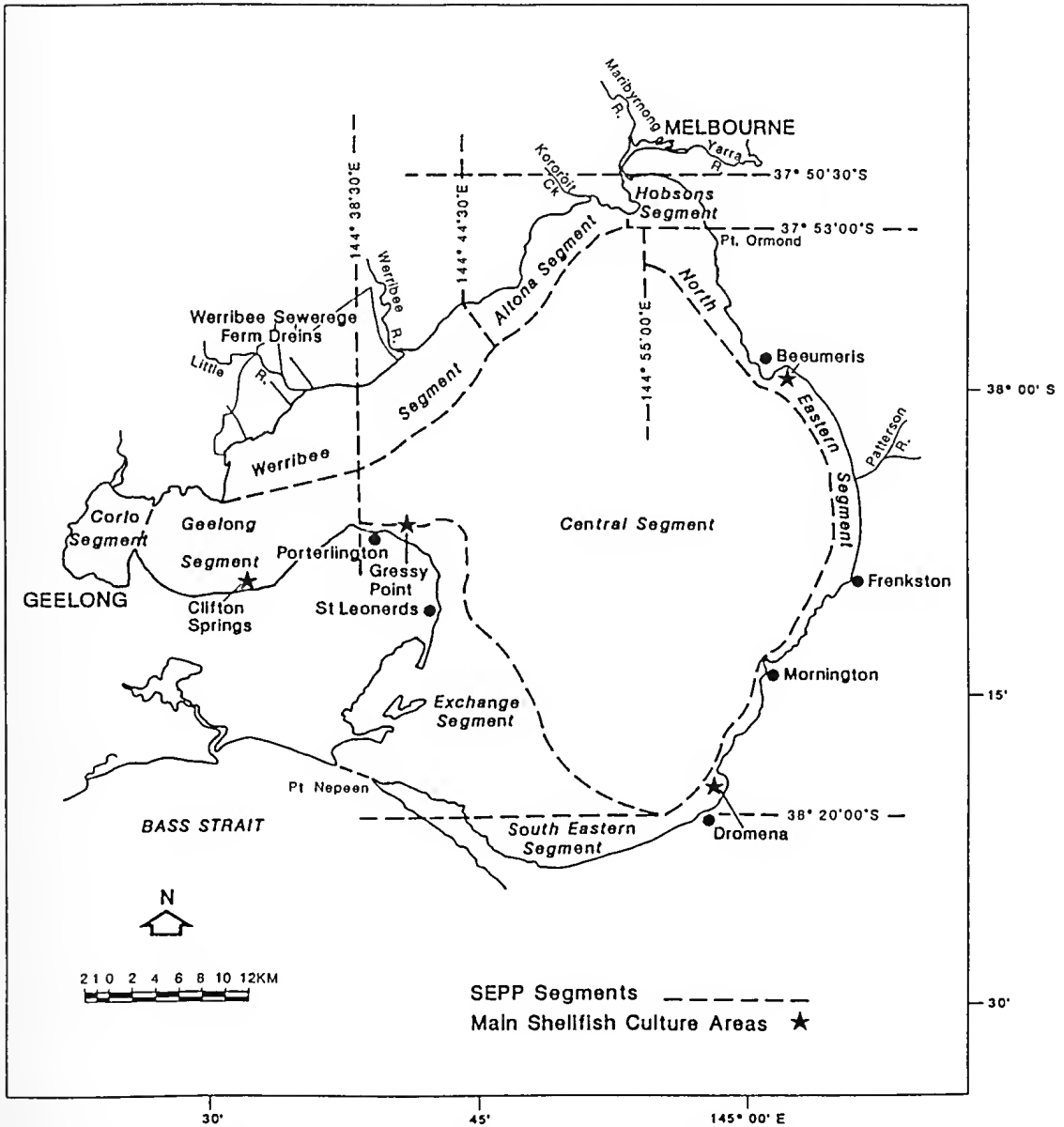
Fig. 1. Map of Port Phillip Bay showing segments defined in the SEPP (The Waters of Port Phillip Bay) (1975) and the approximate positions of main shellfish culture areas.

follows that about 3 times this amount of nitrogen, or 38 tonnes, from the added food supply remains in the ecosystem. In the case of mussels, removal of 500 tonnes wet weight is approximately equivalent to taking 4 tonnes nitrogen from the ecosystem (relationship of live weight:total N weight from Rodhouse & Roden 1987).

Mussel farming may, through a high rate of exeretion of ammonium by the mussels, lead to an increased rate of nitrogen cycling in the water column (Kaspar et al. 1985, Rodhouse & Roden 1987). This could lead to an increased frequency of phytoplankton blooms around mussel farms, but this has not yet been observed (Rodhouse & Roden 1987).

In both types of aquaculture the solid waste will result in increased sedimentation underneath the farms (a salmonid farm may produce about 15 times more sediment than a mussel farm of similar size); however, in the case of passive-feeding aquaculture the increase under the farm is compensated by a decrease in sedimentation of surrounding areas (Folke & Kautsky 1989).

AQUACULTURE ACTIVITIES IN PORT PHILLIP BAY

Apart from a few small-scale proposals for experimental cage culture, aquaculture in Port Phillip Bay has been exclusively of the passive-feeding type, involving filter-feeding molluscs. Two relatively large commercial aquaculture zones have been established at Clifton Springs and Grassy Point, and a number of other small experimental leases have been set up around the Bay (Fig. 1). Significant aquaculture activities are thus taking place in a number of segments outside of the two in which shellfish production for human consumption is listed as a beneficial use in the current policy.

The main species of commercial interest is the blue mussel, *Mytilus edulis planulatus*; there is also limited interest in the flat oyster, *Ostrea angasi*.

Currently commercial shellfish production from mussel farms in the Bay is less than 1000 tonnes per annum; projections for future production extend to between 2000 and 3000 tonnes per annum over the next five years (D. Buckmaster personal communication 1990).

INTERACTION OF AQUACULTURE ACTIVITIES WITH NUTRIENTS IN PORT PHILLIP BAY

In considering aquaculture in the context of the nutrient status of Port Phillip Bay, three questions are pertinent.

1. Is there adequate nutrition available for filter-feeding shellfish?

That a commercial mussel farming industry has been established in the Bay provides some evidence that this is in fact the case. However, information on the maximum "carrying capacity" of areas of the Bay for mussel farming is not yet available.

Experimental growth trials using flat oysters have indicated that sites within Port Phillip Bay are amongst the best in Victoria for growth of this species.

A scallop (*Pecten alba*) fishery operates in the Bay, albeit with extreme fluctuations in population numbers in some years.

There is thus a reasonable case to consider aquaculture as having at least some potential as a beneficial use in Port Phillip Bay.

2. What would be the impact of commercial aquaculture on the nutrient status of the Bay?

If cultured mussel production in the Bay reached the upper projected figure of 3000 tonnes per annum, this harvest would remove about 24 tonnes of nitrogen annually from the Bay.

Were salmon farming to take place in the Bay, an annual production of 1000 tonnes live weight would be a realistic achievable upper limit for the medium term. This production would result in approximately 77 tonnes of nitrogen being added to the Bay each year.

The annual nitrogen load of Port Phillip Bay from all sources is well over 5000 tonnes.

3. What nutrient-related phenomena may have an impact upon aquaculture?

A number of species of phytoplankton, predominantly dinoflagellates, are known to produce various toxins including paralytic shellfish poison (PSP), diarrhetic shellfish poison (DSP), neurotoxic shellfish poison (NSP) and amnesic shellfish poison (ASP), each of which can cause serious illness and sometimes death in human consumers of shellfish so affected. The effects of algal blooms on shellfish have been comprehensively reviewed by Shumway (1990).

The exact relationship between the level of nutrient enrichment of the waterbody, and the type and extent of algal bloom which may occur, is not known.

In addition to toxins affecting human consumers of shellfish, algal blooms can cause mass mortalities of shellfish either through toxic effects or through reduction of dissolved oxygen levels.

Over recent years, two events have been recorded which have been of particular relevance to shellfish culture activities within the Bay.

(a) Bitter tasting shellfish. An extremely bitter taste was acquired by mussels (both cultivated and wild-caught), flat oysters and scallops throughout Port Phillip Bay during September 1987, and continuing through until about mid 1988 (bitter tasting mussels also occurred at a mussel farm at Flinders in Western Port in September 1987; this outbreak of "bitter taste" was less severe than that in Port Phillip Bay). Commercial crops of mussels became unsalcable as a result. Both natural and farmed shellfish stocks

also suffered abnormally high mortalities. An investigation strongly suggested that a bloom of the diatom *Rhizosolenia chunii* was responsible for the bitter taste and subsequent mortality. There was anecdotal evidence of a "bitter taste" outbreak in mussels from Port Phillip Bay in the mid-1970s (Parry et al. 1989).

(b) "Red tides" (information from G. Arnott 1992, unpublished observations). Discolouration of the water in northern parts of Port Phillip Bay was reported in early January 1988, and investigations confirmed the occurrence of Victoria's first recorded "red tide". The alga concerned, *Alexandrium catenella*, was known from overseas work to be capable of contaminating shellfish with a PSP. During the bloom, mussels from certain parts of the Bay contained six times the USFDA limit of PSP. The bloom lasted for about 10 weeks but was always confined to the Hobson's Bay area of Port Phillip Bay. A public health alert warned people not to eat any shellfish from a defined area. No legal commercial supplies of shellfish being sold through retail outlets and restaurants were affected, and no toxins were found in mussels from any commercial or experimental mussel farm in the Bay. In April 1991 and January 1992 (when PSP levels far in excess of those found in 1988 were measured) similar blooms were observed in the northern part of the Bay, and public warnings were again issued.

Several species of toxic dinoflagellates and a toxic diatom are known to occur in Port Phillip Bay. A Port Phillip Bay Biotoxin Surveillance program has been conducted to protect public health from future outbreaks of toxic algal blooms.

AQUACULTURE AS A BENEFICIAL USE IN PORT PHILLIP BAY

Given that active-feeding operations contribute quantities of nutrients into the water, and that concern has already been expressed about the possibility of excess nutrients in the Bay, it may be decided that active-feeding aquaculture should not be considered a beneficial use anywhere within the Bay. Because such activities could be included within the present beneficial use "Production of fish and crustaceans for human consumption", it may be appropriate to rephrase this beneficial use to "Fishing for fish and crustaceans for human consumption".

On the other hand, in the context of nutrients in Port Phillip Bay, there is a strong case that passive-feeding aquaculture should be considered a beneficial use.

The beneficial use "Production of shellfish for human consumption" is not sufficient to define passive-feeding aquaculture, as certain shellfish species (for example, abalone) may be grown using active-feeding techniques. Rephrasing the description to "Production of edible shellfish without addition of nutrients" would better describe this form of aquaculture.

The selection of areas or segments of Port Phillip Bay in which passive-feeding aquaculture should be a beneficial use will depend upon consideration of several aspects of water quality—for example, the potential for metallic and bacterial contamination—in addition to the nutrient status. Not all segments will thus be suitable. While in no areas of the Bay could passive-feeding aquaculture be excluded at present on the grounds of unfavourable (and more specifically excessive) nutrients adversely affecting shellfish, given that the northern portion of the Bay has been affected by "red tides" in recent times, there may be some reservations about listing passive-feeding aquaculture as a beneficial use for this area.

PROTECTING THE BENEFICIAL USE "PRODUCTION OF EDIBLE SHELLFISH WITHOUT THE ADDITION OF NUTRIENTS"

The most difficult part of this exercise is to determine what are the relevant water quality indicators, and what particular objectives should be set to protect this beneficial use. We need to protect:

(a) the shellfish to ensure adequate survival, growth and reproduction; and

(b) the human consumer of the shellfish to minimise the health risk associated with eating the product.

Protection of the shellfish themselves will be in large part accomplished by the setting of water quality objectives for the beneficial use "Maintenance and preservation of natural aquatic ecosystems and wildlife" which is listed for most segments of the Bay. In any case, water quality criteria for protecting the human consumers of shellfish are likely to be as stringent as or more stringent than those for protecting the shellfish.

In the context of nutrients, protection of human consumers of shellfish will be afforded by protection against blooms of toxic phytoplankton.

Ideally, we would need to understand the relationship between phytoplankton blooms and nutrient levels in the waters of Port Phillip Bay in order to develop quantitative nutrient criteria. In examining historical records of red tides or toxicity episodes, we must be on guard for factors which may result in an apparent increase in the frequency of such events, such as increased knowledge and alertness by the scientific community, increased potential to detect toxicity due to close monitoring of shellfish farms, or inadequacy of past sampling techniques (Anderson 1989).

Even after allowing for the influence of the above factors in inflating estimates of the frequency of algal blooms, there is general consensus that these events, worldwide, are becoming more common, more severe, and more widespread. Nutrient enrichment is one of a number of factors thought to enhance algal blooms, and it has been established that there is a direct correlation between the number of red tides and the extent of coastal pollution (particularly from sewage and some forms of industrial wastes; Anderson 1989, Shumway 1990). In view of these findings, it is appropriate that we exercise caution in developing policies for nutrient management, even if we have no clear evidence of cause and effect with regard to nutrient levels and algal blooms in Port Phillip Bay.

Our level of understanding, in common with that elsewhere, still falls short of being able to predict phytoplankton events and the species "mix" when these occur. Until we can do so, a qualitative objective for the indicator "nutrients" such as that used in the SEPP (Waters of Victoria) may be the best we can do: "Waters shall be free of substances in concentration which cause nuisance plant growth or changes in species composition to the detriment of the protected beneficial uses."

To protect public health and the shellfish growing industry, it is essential that a monitoring program is in place to give early warning of unfavourable algal blooms. Shellfish harvesting can then be curtailed until the product is safe to eat. Measurements of nutrient concentrations and loads should also be made to understand better their relationship with the dynamics of algal blooms.

REFERENCES

Anderson, D. M., 1989. Toxic algal blooms and red tides: a global perspective. In *Red Tides—Biology, Environmental Science and Toxicology*, T. Okaichi, D. M. Anderson & T. Nemoto, eds, Elsevier, New York, 11–16.

EPA (Environment Protection Authority, Victoria), 1983. *Manual of Recommended Water Quality Criteria*, 1st edn. Publication No. 165, Environment Protection Authority of Victoria, Melbourne, 247 p.

Folke, C. & Kautsky, N., 1989. The role of ecosystems for a sustainable development of aquaculture. *Ambio* 18: 234–243.

Gowen, R., Brown, J., Bradbury, N. & McLusky, D. S., 1988. Investigations into benthic enrichment, hypernutrification and eutrophication associated with mariculture in Scottish coastal waters. Department of Biological Science, University of Stirling, Stirling, 289 p.

Kaspar, H. F., Gillespie, P. A., Boyer, I. C. & MacKenzie, A. L., 1985. Effects of mussel aquaculture on the nitrogen cycle and benthic communities in Kenepuru Sound, Marlborough Sounds, New Zealand. *Marine Biology* 85: 127–136.

Parry, G. D., Langdon, J. S. & Huisman, J. M., 1989. Toxic effects of a bloom of the diatom *Rhizosolenia chunii* on shellfish in Port Phillip Bay, southeastern Australia. *Marine Biology* 102: 25–41.

Rodhouse, P. G. & Roden, C. M., 1987. Carbon budget for a coastal inlet in relation to intensive cultivation of suspension-feeding bivalve molluscs. *Marine Ecology, Progress Series* 36: 225–236.

Shumway, S. E., 1990. A review of the effects of algal blooms on shellfish and aquaculture. *Journal of the World Aquaculture Society* 21: 65–104.

Woodward, I., 1989. *Finfish Farming and the Environment—A Review*. Technical Report No. 35, Department of Sea Fisheries, Tasmania, Taroona, 43 p.

Victorian Government, 1987a. *Victoria—The Next Decade*. Victorian Government Printer, Melbourne, 283 p.

Victorian Government, 1987b. *Environment Protection Act 1970*. Victorian Government Printer, Melbourne, 118 p.

REVISION OF THE FAMILY LINEOLARIIDAE ALLMAN, 1864 (HYDROZOA: HYDROIDA)

Jeanette E. Watson

Honorary Associate, Museum of Victoria, 285 Russell Street, Melbourne, Victoria 3000

Watson, Jeanette E., 1992:09:30. Revision of the family Lineolariidae Allman, 1864 (Hydrozoa: Hydroida). *Proceedings of the Royal Society of Victoria* 104: 81–87. ISSN 0035-9211.

The family Lineolariidae Allman, 1864 is redefined and the known species are redescribed. The genus *Lineolaria* Hincks, 1861 is endemic to south-eastern Australia, and the new genus *Nicoliana* is proposed for *Lineolaria gravierae* Millard, 1975 from southern Africa. *Lineolaria parasitica* Antsulevich, 1987 and *Agglutinaria operculata* Antsulevich, 1987 from the Sea of Okhotsk are excluded from the family. *Lineolaria spinulosa* Hincks, 1861 and *Nicoliana gravierae* are both obligate epiphytes of seagrasses, and *Lineolaria flexuosa* Bale, 1884 occurs only on algae. Evolutionary implications and the distribution of the family are discussed.

THE FAMILY Lineolariidae presently comprises six species in two genera: *Lineolaria spinulosa* Hincks, 1861 (type species), *L. flexuosa* Bale, 1884, *L. inarmata* Blackburn, 1938, *L. gravierae* Millard, 1975, *L. parasitica* Antsulevich, 1987 and *Agglutinaria operculata* Antsulevich, 1987. *L. spinulosa, L. flexuosa* and *L. inarmata* are known from south-eastern Australia (Hincks 1861, Bale 1884, Bartlett 1907, Blackburn 1938, Watson 1973), and *L. flexuosa* has been reported also from New Zealand (Trebilcock 1928, Ralph 1958). *L. gravierae* is known from Madagascar and Mozambique (Gravier 1970, Millard 1975), and *L. parasitica* and *A. operculata* from the Sea of Okhotsk (Antsulevich, 1987).

Hincks (1861) (and later Stechow 1923) assigned *Lineolaria* to the Sertulariidae, but Allman (1864) introduced the family Lineolariidae to accommodate the genus and this classification was followed by Ralph (1958), Watson (1973) and Antsulevich (1987). Although Millard (1975: 133) and Bouillon (1985: 130) referred *Lineolaria* to the Campanulinidae, their definitions of the genus included a hydrothecal operculum "present or absent, when present membranous . . .", thus implying the possibility of a simple opercular flap, a structure inconsistent with the segmented operculum diagnostic of the Campanulinidae. In his original description of *Lineolaria*, Hincks (1861) made no mention of a hydrothecal operculum. I have examined Hincks's type material of *L. spinulosa* in the collection of the Natural History Museum, London (BMNH 1899.5.1.219) and, although no operculae are visible, their absence is readily explained by loss through drying. Young hydrothecae of fresh material that I have collected from lower Port Phillip Bay all possessed an elliptical bilobed margin closed by a delicate membranous flap that is torn aside upon emergence of the young hydranth.

Antsulevich's (1987) diagnosis of the Lineolariidae includes a rudimentary hydrothecal peduncle to accommodate *L. parasitica* and *A. operculata* in the family. However, if Hincks's original concept of a sessile hydrotheca is to be maintained, these two species must be excluded. The inoperculate *L. parasitica* appears to have closer affinities with the Lafoeidae than with the Lineolariidae, while *A. operculata* with its conical operculum may be more closely related to *Cuspidella, Eginmdella* or *Lafoeina*. Neither species, however, can be referred with confidence to any known genus until the reproductive structures are found.

A redefinition of the scope of the families Lineolariidae and Campanulinidae thus becomes necessary. If *Lineolaria* as understood by Millard (1975) and Bouillon (1985) is to remain in the Campanulinidae, then the Lineolariidae and Campanulinidae must be regarded as synonymous, with the name Lineolariidae taking precedence (Calder 1991). However, if the Lineolariidae is redefined to accommodate the operculum, the family may then be retained as distinct from the Campanulinidae. Since *Lineolaria* possesses a simple operculum in the type species, the new genus *Nicoliana* is introduced here to accommodate the southern African species with a segmented operculum.

Family LINEOLARIIDAE Allman, 1864, amended

Diagnosis. Small thecate hydroids with stolonal colonies growing on an underlying sheet of per-

isarc. Hydrotheca sessile, deep, tubular to sac-
cate, with an upturned, untoothed or lobate mar-
gin; operculum a simple flap or conical, of
converging segments demarcated from the mar-
gin. Hydranth slender and extensile, with a ring
of filiform tentacles. Nematophores present or
absent. Gonotheca sessile, gonophore a fixed
sporosac.

Lineolaria Hincks, 1861, amended

Type species. Lineolaria spinulosa Hincks, 1861.

Diagnosis. Colonies stolonal, hydrotheca sessile,
deep, cylindrical to saccate, margin upturned,
elliptical to circular with two opposite lobes and
an operculum of a simple flap. Nematophores
absent. Gonotheca sessile, gonophore a fixed
sporosac.

Lineolaria *from Australia and New Zealand.* The
type material of *L. spinulosa* is epiphytic on
dried leaves of the seagrass *Cymodocea antarc-
tica* (= *Amphibolis antarctica* (Labill.) Sonder et
Aschers) and is labelled "Geelong, Australia". It
is from a "parcel of sea-weed . . . from the neigh-
bourhood of Melbourne and Geelong" (Hincks
1861). The type locality given is probably incor-
rect since the nearest occurrence of *A. antarctica*
to Melbourne and Geelong is in lower Port Phil-
lip Bay and Bass Strait. The species has been
recorded from the same substrate at other lo-
calities by Bale (1884), Bartlett (1907), Black-
burn (1938) and Watson (1973 and present
study). It is the most abundant hydroid epiphyte
of *A. antarctica* (Watson in press) and is an
equally common epiphyte of *Posidonia australis*
(Hooker) and *P. sinuosa* Kuo & Cambridge in
south-eastern Australia (J.E.W. unpubl.). De-
spite extensive searching I have not found the
species on other substrates nor on the same
species of seagrasses in south-western Aus-
tralia.

Lineolaria *flexuosa* is a south-eastern Aus-
tralian algal epiphyte, found in this study to be
chiefly associated with the common brown alga
Sargassum spp. and the red alga *Rhodymenia. L.
flexuosa* has been recorded in Australia from the
environs of Port Phillip Bay (Bale 1884, Bartlett
1907) and from the Sir Joseph Banks Islands in
Spencer Gulf (Blackburn 1938). The only pre-
vious record of substrate is of a specimen "on
algae" from Williamstown, Victoria (Bale
1884). Material on algae from West Island,
South Australia, identified as *L. spinulosa* by
Shepherd & Watson (1970), is also probably *L.
flexuosa.* Despite the paucity of records I have

found *L. flexuosa* to be a moderately common
algal epiphyte; it is not, however, as abundant as
L. spinulosa.

Trebilcock (1928) recorded *L. flexuosa* from
Stewart Island in southern New Zealand without
describing the specimen or commenting upon its
habitat. Despite careful search of the Trebilcock
collection and other material in the Museum of
Victoria, I have found no specimen correspond-
ing to Trebilcock's data. Ralph (1958) also re-
corded *L. flexuosa* from Cape Maria Van
Diemen, New Zealand, growing on the stem of
Synthecium. Because the specimen was sterile
she described and figured a gonotheca from a
microslide preparation of *L. flexuosa* from the
Sir Joseph Banks Islands, Australia, prepared by
M. Blackburn and now in the collection of the
Museum of Victoria. I have examined two
microslides of the Cape Maria Van Diemen
specimen (loaned by Dr P. M. Ralph) and found
that the hydrothecae, all of which are partially
free of the substrate, have an entire, more or less
circular margin, not the distinctively lobed,
usually elliptical margin typical of *Lineolaria.*
None of the specimens shows any evidence of
there having been an operculum. Since partially
adnate, cylindrical hydrothecae with circular
margins and without operculae are typical of
Filellum, I believe that Ralph's specimens
should be referred to that genus. This view is
supported by the epizoic habit of the specimen
on *Synthecium,* a favoured substrate of *Filellum*
in southern Australian waters (J.E.W., unpubl.).
This is in contrast with the epiphytic habit of the
Lineolariidae.

Lineolaria *inarmata* has been recorded only
once, from seagrasses at the type locality at the
Sir Joseph Banks Islands in southern Spencer
Gulf, South Australia. I have examined the holo-
type (NMV F57878) and paratype (NMV
F57879) microslides (Canada balsam mounted)
in the collection of the Museum of Victoria and
found the specimen to be closely similar to *L.
spinulosa.* Blackburn (1938) distinguished
between the two species chiefly on the absence of
the basal hydrothecal spine in *L. inarmata* and
the poorly developed marginal lobes of the
hydrotheca. Detailed examination revealed that
both the basal spines and the marginal lobes
were in fact present but had been crushed in
mounting. Blackburn further distinguished *L.
inarmata* from *L. spinulosa* on ecological
grounds, stating that *L. spinulosa* occurred only
on *Cymodocea* (= *Amphibolis*), whereas *L. inar-
mata* was found only on *Posidonia.* This differ-
entiation is no longer valid as *L. spinulosa* is now

found to be an equally common epiphyte of *Posidonia* in the Great Australian Bight (Watson 1973) and many other southern Australian localities (J.E.W. unpubl.). Thus *L. inarmata* is here considered a synonym of *L. spinulosa*.

The redescriptions of *L. spinulosa* and *L. flexuosa* given below are from fresh and preserved material and microslides. Measurements of both species are given in Table 1. Material used in this study has been deposited in the Museum of Victoria (registration numbers prefixed NMV).

Lineolaria spinulosa Hincks, 1861

Fig. 1A,B

Lineolaria spinulosa Hincks 1861: 280, pl. 8.—Allman 1864: 36.—Bale 1882: 8.—Bale 1884: 61, pl. 1, figs 10, 11, pl. 19, fig. 38.—Lendenfeld 1885a: 405.—Lendenfeld 1885b: 622.—Lendenfeld 1887: 18.—Bartlett 1907: 41.—Watson 1973: 165.
Lineolaria inarmata Blackburn 1938: 321, figs 4–8.

Material and records. NMV F51784, Queenscliff, Victoria, on *Amphibolis antarctica*, 3 m, J. E. Watson, 4 Jan. 1987, preserved material. NMV F51785, Gulf St Vincent, South Australia, on *Posidonia*, 16 m, S. A. Shepherd, 10 Nov. 1968, microslide.

Description. Hydrorhiza broad and flat, reticulated; strongly adherent to the substrate. Hydrothecae borne directly on the hydrorhiza, usually alternate, normal to the stolon and about 0.5–1 mm apart. Hydrotheca rectangular, perisarc with minute transverse striations, strongly adnate to the substrate for most of length then bending sharply upwards and becoming free in the distal fifth, slightly inflated proximally, narrowing slightly behind margin. Margin oval with two small lateral lobes, immature hydrotheca closed by a delicate membranous flap. Base of the hydrotheca with a strong, erect chitinous spine at junction with hydrorhiza, a small crease in the stolon opposite the spine.

Hydranth with about 16 tentacles, capable of withdrawing deeply into the hydrotheca.

Colonies dioecious, gonothecae large, abundant, usually nestled beside the hydrothecae between stolonal reticulations, male and female similar in shape and size, flattened, irregularly ovate, adnate to the substrate by a peripheral flange about 0.1 mm wide. Aperture distal, circular or sub-circular, facing upwards with a thickened rim and closed by a membranous operculum. Surface of gonotheca with 16–30 small chitinous spines in three or four vaguely defined longitudinal rows, a mass of tissue surrounding the base of each spine. Gonophore irregularly ovate, the female comprising up to 15 ova arranged in two rows.

Colour. Trophosome transparent and colourless, so that the colony is almost invisible on the substrate. Gonophores cream-coloured.

Remarks. L. spinulosa is a minute hydroid, the colonies scarcely exceeding a height of 0.5 mm above the substrate. Contact with the substrate is by means of a very delicate, strongly adherent film of perisarc that underlies the entire colony. The thorn-like spines at the base of the hydrothecae are the same as those on the gonotheca. These robust, hollow chitinous structures are closed at the tip; unlike the tubular nematophores of *Nicoliana gravierae*, they do not con-

	L. spinulosa		*L. flexuosa*	
	Range	Mean	Range	Mean
Hydrorhiza:				
maximum width excluding flange		0.17		0.08
Hydrotheca:				
length adnate	0.27–0.35	0.30	0.23–0.28	0.25
length free	0.06–0.09	0.08	0.04–0.08	0.06
maximum width	0.13–0.18	0.16	0.09–0.13	0.11
width at aperture	0.13–0.17	0.15	0.08–0.11	0.09
Gonotheca:				
length including flange	1.25–1.50	1.40	0.88–1.00	0.94
width including flange	0.63–0.75	0.68	0.55–0.75	0.65
diameter of aperture	0.14–0.18	0.16	0.15–0.20	0.18
maximum length of spine		0.08		0.08
width of spine at base		0.04		0.05

Table 1. Comparative measurements (mm) of *Lineolaria spinulosa* and *Lineolaria flexuosa* (n = 10, both species).
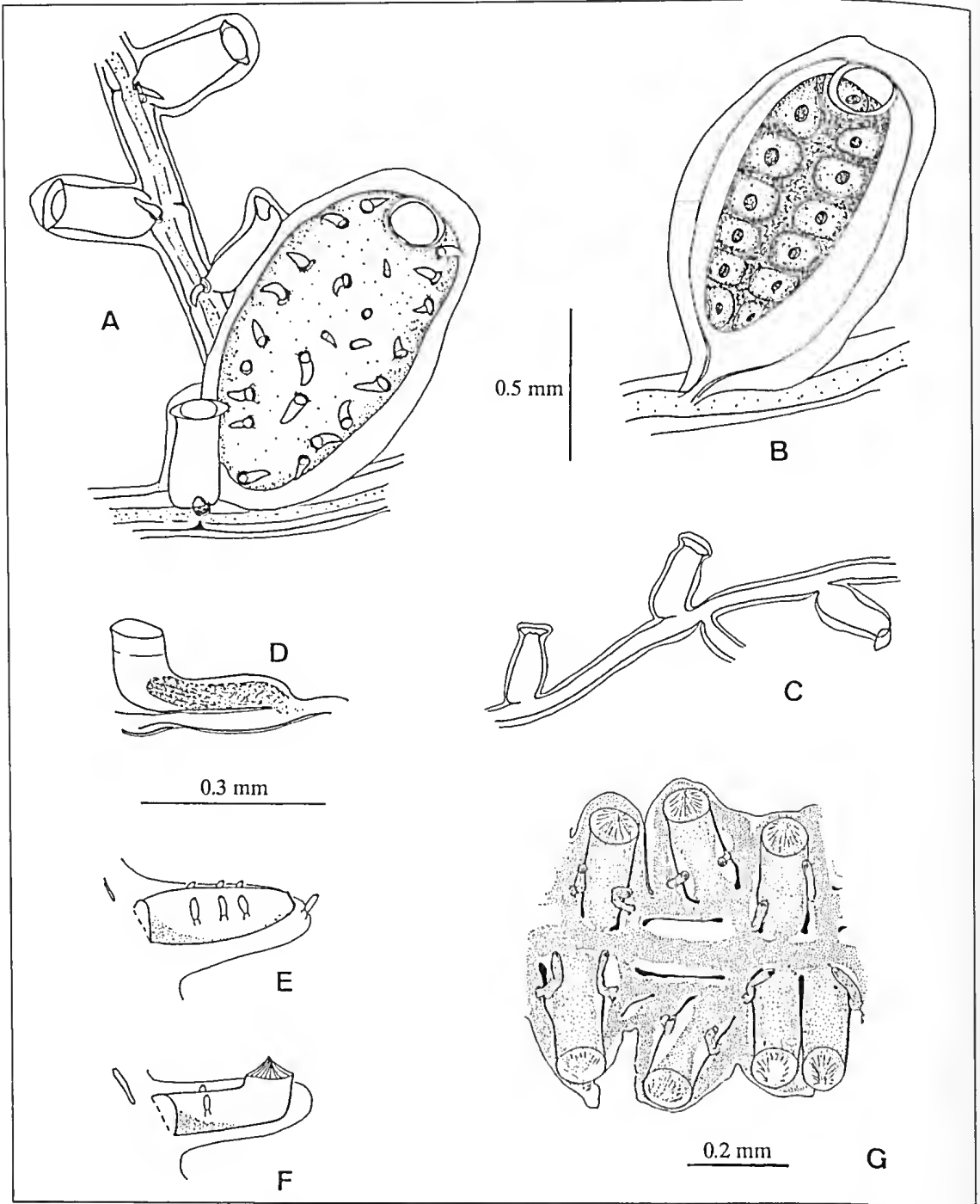
Fig. 1. A, B, *Lineolaria spinulosa*, colony from *Amphibolis antarctica*, Queenseliff, Victoria. A, part of eolony with empty gonotheea. B, female gonophore inside gonotheea (gonotheeal spines not shown). C, D, *Lineolaria flexuosa*, colony from *Sargassum*, Western Port, Vietoria. C, part of sterile colony. D, hydrotheea without marginal lobes, resembling *Filellum*. E–G, *Nicoliana gravierae*. E, lateral view of gonotheea. F, lateral view of hydrotheea. E and F after Millard 1975. G, eolony, after Gravier 1970 (seale not given).

tain nematocysts. It is possible that they were once also nematophores but with evolutionary loss of nematocysts have degenerated into spines. These may now serve as structures for passive defence of the colony.

L. spinulosa is an extremely fecund species, the colonies becoming fertile soon after earliest stolonisation. The marked irregularities seen in the walls of the gonothecae usually result from obstructions to free growth among the hydrorhizal reticulations.

Lineolaria flexuosa Bale, 1884

Fig. 1C, D

Lineolaria flexuosa Bale 1884: 62, pl. 1, figs 7–9.— Bale 1887: 19.—Lendenfeld 1885a: 405.—Lendenfeld 1885b: 622.—Lendenfeld 1887: 18.—Hartlaub 1905: 617.—Bartlett 1907: 41.— Trebilcock 1928: 8.—Blackburn 1938: 321.— Blackburn 1942: 111. —Smith & Watson 1969: 109.
non *Lineolaria flexuosa.*—Ralph 1958: 325, fig. 8a–h. —Shepherd & Watson 1970: 140.

Material and records. NMV F51786, Popes Eye Reef, Port Phillip Bay, Victoria, on *Zonaria*, 7 m, J. E. Watson, 31 May 1976, microslide. NMV F51787, Eagle Rock, Western Port, Victoria, on *Sargassum*, 3 m, J. E. Watson, 11 Nov. 1968, microslide. NMV F51788, Crawfish Rock, Western Port, Victoria, on *Rhodymenia*, 8 m, J. E. Watson, 26 Apr. 1969, microslide.

Description. Hydrorhiza flattened, adherent to substrate, with a small peripheral flange. Hydrothecae usually alternate and set at an acute angle to the stolon or parallel with it, connected to the stolonal canal through a wide orifice. Hydrotheca rectangular to saccate, widest about the middle, adnate to substrate for most of length, turning sharply upwards in the distal fifth. Margin delicate, circular to elliptical, with a pair of lateral lobes, aperture of immature hydrotheca closed by a delicate membranous flap.

Colonies dioecious, gonotheca large, situated beside a hydrotheca, male and female similar in shape and size, irregularly ovate, strongly flattened and adnate to the substrate by a wide peripheral flange, aperture distal, circular to subcircular, with thickened rim, the surface with small chitinous spines.

Colour. In life, colonies yellow or white, gonophores cream-coloured.

Remarks. In lateral view, the hydrothecae of sterile colonies of *L. flexuosa* may be mistaken for *Filellum*, particularly if the margins of some hydrothecae are circular and lack lateral lobes (Fig. 1D). Marginal lobes are, however, present in most hydrothecae; these are best seen when viewed from above.

The most important difference between *L. spinulosa* and *L. flexuosa* is the presence of the basal hydrothecal spine in the former and its absence from the latter.

The hydrorhiza of *L. flexuosa* is narrower than that of *L. spinulosa* and is usually undulating, following the irregularities of the algal thallus, whereas that of *L. spinulosa* is flat, more orderly, and neatly aligned with the reticulating cells of the seagrass leaf.

The hydrothecae of *L. flexuosa* usually grow at an acute angle to, or sometimes parallel with the hydrorhiza, whereas those of *L. spinulosa* almost invariably project at right angles to the hydrorhiza. These structural differences may be environmentally induced and are thus not of specific importance. The hydrothecae of the two species are similar in shape but those of *L. spinulosa* are usually slightly larger. In both species usually only the distal fifth is bent upwards from the substrate, but in some hydrothecae one-third may be free.

Both species grow on a basal sheet of perisarc which separates the entire colony from the substrate. The underside of the hydrorhiza of *L. spinulosa* has numerous small, hook-like extensions that penetrate between the cells of the seagrass leaf, thus providing additional anchorage to the substrate. Although also present in *L. flexuosa*, hydrorhizal hooks are usually less well developed than in *L. spinulosa*, and they may be absent altogether.

There are no features that readily distinguish the gonothecae of the two species, except that the mature gonotheca of *L. spinulosa* is usually somewhat larger and has fewer spines than that of *L. flexuosa*.

When considered together these points of difference are sufficiently constant to warrant separation of the two species at present.

Because of the minute size and transparency of the hydrothecae, both species are easily overlooked.

Nicoliana gen. nov.

Type species. Lineolaria gravierae Millard, 1975.

Diagnosis. Colonies stolonal, hydrotheca sessile, deep, cylindrical to saccate, margin upturned, circular, with a peaked operculum of converging segments. Nematophores present. Gonotheca sessile, gonophore a fixed sporosac.

Remarks. Nicoliana differs from *Lineolaria* in

its segmented, conical operculum and the nematophores flanking the hydrotheca and gonotheca.

Nicoliana gravierae (Millard, 1975)

Fig. 1E–G

Lineolaria gravierae Millard 1975: 134, fig. 43H.
Lineolaria sp.—Gravier 1970: 144, figs 11, 13A.— Gravier-Bonnet 1972: 8.—Millard & Bouillon 1974: 22, fig. 2D.

Remarks. Nicoliana gravierae was described in detail by Millard (1975); it is figured here but not redescribed. It is one of the dominant epiphytic hydroids on the leaves of the seagrasses *Cymodocea serrulata* and *C. ciliata* from Madagascar (Gravier 1970, Gravier-Bonnet 1972), and is also reported from Cymodocea in Mozambique (Millard & Bouillon 1974, Millard 1975).

DISTRIBUTION AND EVOLUTION OF THE LINEOLARIIDAE

The success of *L. spinulosa* as a seagrass epiphyte suggests a long history of association with the Australian seagrass flora which may date back to the ancestral *Cymodocea serrulata* meadows of the Indo-Pacific Miocene. The present disjunct distribution and evolutionary isolation of the Lineolariidae between southeastern Australia and southern Africa could be explained by later scattering of the shelf seagrass flora through continental break-up (Laurent & Laurent 1926, Larkum & den Hartog 1989). The apparent absence of the Lincolariidae from the eastern shores of the Indian Ocean in southwestern Australia is nevertheless puzzling and requires further explanation.

L. flexuosa in south-eastern Australian waters may represent a case of incipient speciation from the ancestral *L. spinulosa* stock, leading to suppression and loss of several morphological characters. The habitat on algae is analogous to that of *L. spinulosa* on seagrasses since it also occurs in shallow coastal environments, often adjacent to seagrass meadows.

ACKNOWLEDGEMENTS

REFERENCES

ALLMAN, G. J., 1864. On the construction and limitation of genera among the Hydroida. *Annals and Magazine of Natural History*, Series 3, 13: 345–380.

ANTSULEVICH, A. E., 1987. *Gidroidy shelfa Kurilskikh Ostrovov.* Akademiya nauk SSSR, Zoologicheskii Institut, Leningrad, 163 p.

BALE, W. M., 1882. On the Hydroida of south-eastern Australia, with descriptions of supposed new species, and notes on the genus *Aglaophenia. Journal of the Microscopical Society of Victoria* 2: 15–48, pls 12–15.

BALE, W. M., 1884. *Catalogue of the Australian Hydroid Zoophytes.* Australian Museum, Sydney, 117 p.

BALE, W. M., 1887. The genera of the Plumulariidae with observations on various Australian hydroids. *Proceedings of the Royal Society of Victoria* 23: 73–110.

BARTLETT, G. C., 1907. Notes on hydroid zoophytes. *Geelong Naturalist* 3: 35–45.

BLACKBURN, M., 1938. The Hydrozoa of the Sir Joseph Banks Islands. *Proceedings of the Royal Society of Victoria* 50: 312–328.

BLACKBURN, M., 1942. A systematic list of the hydroids of South Australia with a summary of their distribution in other seas. *Transactions of the Royal Society of South Australia* 66: 104–118.

BOUILLON, J., 1985. Essai de classification des hydropolypes–hydroméduses (Hydrozoa–Cnidaria). *Indo-Malayan Zoology* 2: 29–243.

GRAVIER, N., 1970. Étude des Hydraires épiphytes des phanérogames marines de la région de Tuléar (sud-ouest de Madagascar). *Recordes Travaille Statione Marine Endoume* 10: 111–161.

GRAVIER-BONNET, N., 1972. Hydroïdes épiphytes de trois phanérogames marines en provenance de Nossi-Bé (NW de Madagascar). *Tethys* (Supplement) 3: 3–10.

HARTLAUB, C., 1905. Die Hydroiden der magalhaenischen Region und chilenischen Küste. *Zoologische Jahrbücher* (Supplement) 6: 497–714.

HINCKS, T., 1861. A catalogue of the zoophytes of south Devon and south Cornwall. *Annals and Magazine of Natural History*, Series 3, 8: 152–161, 251–262, 290–297, 360–366.

HINCKS, T., 1862. A catalogue of the zoophytes of south Devon and south Cornwall. *Annals and Magazine of Natural History*, Series 3, 9: 22–30.

LARKUM, A. W. D. & DEN HARTOG, C., 1989. Evolution and biogeography of seagrasses. In *Biology of Seagrasses: a Treatise on the Biology of Seagrasses with Special Reference to the Australian Region*, A. W. D. Larkum, A. J. McComb & S. A. Shepherd, eds, Elsevier, 112–145.

LAURENT, L. & LAURENT, J., 1926. Étude sur une

plante fossile des dépôts du Tertaire marine du sud de Célébes, *Cymodocea micheloti* (Wat.) nob. *Jaarboek van het mijnwezen in Nederler-landsch-Oost-Indië* 54: 167–190.

LENDENFELD, R. VON, 1885a. The Australian hydromedusae. Part 3. The 1st suborder Hydropolypinae. The Blastopolypidae. *Proceedings of the Linnean Society of New South Wales* 9: 401–420, pls 7, 8.

LENDENFELD, R. VON, 1885b. The Australian hydromedusae. Part 5. The Hydromedusinae, Hydrocorallinae and Traehymedusae. *Proceedings of the Linnean Society of New South Wales* 9: 581–634, pls 20–29.

LENDENFELD, R. VON, 1887. *Descriptive Catalogue of the Medusae of the Australian Seas,* part 2, *Hydromedusae.* Australian Museum, Sydney, 49 p.

MILLARD, N. A. H., 1975. Monograph of the Hydroida of South Afriea. *Annals of the South African Museum* 68: 1–513.

MILLARD, N. A. H. & BOUILLON, J., 1974. A collection of hydroids from Moçambique, East Afriea. *Annals of the South African Museum* 65: 1–40.

RALPH, P. M., 1958. New Zealand theeate hydroids. Part 2. Families Lafoeidae, Lineolariidae, Haleeiidae and Syntheciidae. *Transactions of the Royal Society of New Zealand* 85: 301–356.

SHEPHERD, S. A. & WATSON, J. E., 1970. The sublittoral ecology of West Island, South Australia: 2. The association between hydroids and algal substrate. *Transactions of the Royal Society of South Australia* 94: 139–146.

SMITH, B. J., & WATSON, J. E., 1969. A short history of William Mountier Bale FRMS (1851–1940). Victorian natural history pioneer, his bibliography and new names list. *Victorian Naturalist* 86: 105–110.

STECHOW, E., 1923. Zür Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete. 2. Teil. *Zoologische Jahrbücher* (Systematik) 47: 29–270.

TREBILCOCK, R. E., 1928. Notes on New Zealand Hydroida. *Proceedings of the Royal Society of Victoria* 41: 1–31.

WATSON, J. E., 1973. Pearson Island expedition 1969.—9. Hydroids. *Transactions of the Royal Society of South Australia* 97: 153–200.

WATSON, J. E., 1992 (in press). The hydroid community of *Amphibolis* seagrasses in southeastern and south-western Australia. *Scientia Marina* 56.

REGENERATION OF *ACACIA MELVILLEI* IN PART OF SEMI-ARID SOUTH-EASTERN AUSTRALIA

Andrew L. Batty and R. F. Parsons

Botany Department, La Trobe University, Bundoora, Victoria 3083

Batty, A. L. & Parsons, R. F., 1992:09:30. Regeneration of *Acacia melvillei* in part of semi-arid south-eastern Australia. *Proceedings of the Royal Society of Victoria* 104: 89–97. ISSN 0035-9211.

The regeneration of the tree *Acacia melvillei* (yarran) was studied in a semi-arid area within 100 km of Balranald, south-west New South Wales using size-class analysis and seedling transplants into a remnant stand. Almost total regeneration failure was found in all pastoral areas except for a few sites known or presumed to have experienced intermittently low browsing pressure. At these sites, two recruitment episodes are tentatively assigned to the 1950s and to 1973–1975. In dryland cropping areas, root damage by cultivation can produce profuse regeneration by root suckering. This is seen as an artefact of European land use practices. The transplants showed that seedling establishment can be strongly limited by low soil moisture in spring and summer and by rabbit browsing. Retaining *A. melvillei* in biological reserves will require strict rabbit control. In addition, pastoral areas will require stock removal during and after the wet years needed for regeneration.

IN SEMI-ARID and arid Australia, research is producing a growing list of tree species whose regeneration is strongly inhibited or prevented by browsing of seedlings and suckers by introduced mammals (Chesterfield & Parsons 1985, Auld 1990, Parsons 1990). While the list includes a number of *Acacia* species (Auld 1990), many *Acacia* spp. have yet to be studied. Ability to sucker is not well documented and the relative importance of seedlings and suckers in the perpetuation of stands is often not understood. Here we investigate regeneration from seedlings and suckers under a variety of browsing and clearing regimes in *Acacia melvillei* Pedley (yarran), a community dominant in parts of inland Queensland, New South Wales and Victoria.

THE SPECIES

Acacia melvillei has only recently been distinguished from *A. homalophylla* Cunn. ex Benth. Both species are widespread throughout the southern part of inland Queensland and inland New South Wales, with more limited occurrences in northern Victoria (Pedley 1978).

Mature pods are needed to distinguish the two species reliably. While these were not available during the present study, all reliably named herbarium specimens seen from our study area at MEL and NSW were labelled *A. melvillei* (M. Fox personal communication; our own data). This, and the number of flowers per head on our plants, strongly suggest that all the yarran plants we saw were *A. melvillei*.

In our study area, *A. melvillei* occurs as the sole dominant of a woodland community on reddish loam flats.

THE STUDY AREA

All sites were within 100 km of Balranald (Fig. 1), where the climate is the cool, semi-arid BSk type (Dick 1975) and mean annual rainfall ranges from about 280 mm to 330 mm. Grazing by stock (mainly sheep) and by rabbits has been widespread since the 1870s (Condon 1983, New South Wales Soil Conservation Service 1990). Sites were chosen to encompass the drier, pastoral areas in the north and the wetter, dryland cropping areas in the south (Fig. 1, Table 1). Few sites could be found with a history of low grazing pressure (known for site 4; inferred for site 6, see Table 1). Sampling was concentrated in those few areas where some regeneration had occurred in the last 40 years or so (sites 4 to 10, Table 1). Many stands lacking regeneration were present in the area; only three of these were sampled (sites 1 to 3, Table 1). It proved very difficult to obtain records of grazing history because the leases for many pastoral areas have changed hands in the last ten years or so.

METHODS

Size class analysis

To provide regeneration data rapidly over a wide area, *Acacia melvillei* stem girths were measured in single, large, unreplicated, subjec-
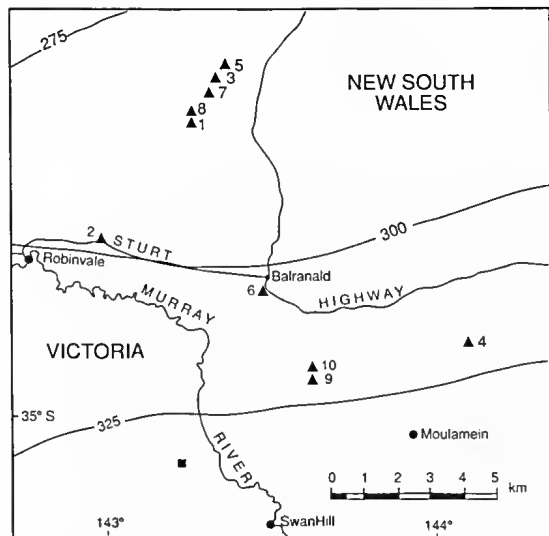
Fig. 1. Location of the study sites and mean annual isohyets (mm) in south-west New South Wales and north-west Victoria. Triangles = size class analysis sites; square = seedling survival site.

tively chosen plots, following previous work (Crisp & Lange 1976, Chesterfield & Parsons 1985). Stems were measured 15 cm above ground to avoid buttressing. In multistemmed plants, stems less than 5 cm in girth were ignored; for those greater than 5 cm girth, the girths were converted to cross-sectional areas and these added to obtain total girth (Fritts 1969). This seemed the best approach given that, in some of the oldest stands, up to half the trees were multistemmed, not single-stemmed. Plot size was varied (Table 1) so that about 75 trees were sampled in each (including dead ones). If fewer than 75 were present, whole populations were sampled.

Seedling survival

Effects of climate and rabbit grazing on seedling establishment were examined in Flora Reserve G67, a 23 ha stock-free area (Victoria: Land Conservation Council 1989) carrying some *Acacia melvillei* trees at Yarraby north-west of Swan Hill (Fig. 1).

Rabbit-proof cages were made and a field trial set up as 3 planting dates × 2 treatments (caged and uncaged) × 4 replicates. All plots were at least 12 m from the nearest tree. Seedlings were raised in a glasshouse using *Acacia melvillei* seed collected on 15 January 1990 from between Goschen and Ultima (map reference Nyah 7527,

714 228). On each date (6 weeks apart), plots were planted with four-week-old seedlings with cotyledons and one to two fully expanded leaves. They were planted open-rooted in four rows of three at 10 cm spacing, into plots from which all plants (mainly exotic annual grasses) had been removed. On planting day, each plot received 10 L of water, 6 L before planting and 4 L after. No further water was applied. The site was a reddish loam flat.

On later visits, seedlings were recorded as being: (a) live; (b) dead-browsed—these had the shoots bitten off, generally below the cotyledons, and none resprouted; or (c) dead-unbrowsed— whole shoot still present. A minority (1%) had disappeared completely for reasons unknown. The trial was terminated on 9 September 1991, 5 weeks after the final planting. The data were analyzed by chi-squared tests.

The field work was carried out between February and September 1991 except for brief checks on seedling survival on 30 November 1991 and 25 March 1992; voucher specimens have been lodged at La Trobe University Botany Department Herbarium (LTB).

RESULTS

Size class analysis

The girth histograms can be readily divided into four groups based on the varying sizes of dead and alive trees (Fig. 2). Populations in group one showed abundant evidence of sheep and rabbit grazing and a general absence of regeneration. Most *Acacia melvillei* individuals were dead (Figs 2, 3A) and there was an absence of individuals in size classes smaller than 80–100 cm except for two plants in the 10–20 cm size class at site 1. These had grown up through the dense canopies of chenopod shrubs which had presumably acted as nurse plants. Excavation showed both to be seedlings, not suckers.

Group one contains an average of 8% live plants; these are old, with decumbent, collapsing stems and usually less than half their branches left alive. In the pastoral parts of the study area, these degenerating stands mostly devoid of regeneration are by far the most common type seen; e.g. various areas around sites 1, 2, 3, 4 and 7. In a number of cases, all that remains of *Acacia melvillei* stands are a few dead and fallen trunks, lying on virtually bare loamy flats surrounded by healthy mallee vegetation on higher ground.

Group	Site	Location	Grid reference	No. of plants measured	Area sampled (ha)	Grazing/clearing	Records of regeneration	Presence of regeneration
1	1	Bidura Station	YH016015	59	1.5	Sheep, rabbits	None	No
	2	Topra Plains Station	YG833759	63	1.3	Sheep (heavy), rabbits	None	No
	3	Hillview Station	YH026026	79	0.9	Sheep, rabbits (heavy)	None	No
2	4	Tchelery Soil Conservation Service Experimental Area (71 ha)	BB479418	77	0.6	Rabbits (periodic), no sheep since 1952	1952–1953	Yes
	5	Hillview Station home paddock	YH026029	80	0.3	Sheep, rabbits	Early 1950s	Yes
	6	Public stock reserve S of Balranald	YG345613	80	0.2	Sheep (periodic), rabbits	None	Yes
3	7	Wintong Station	YH024023	55	1.0	None available	None	Yes
	8	Bidura Station	YH017016	83	0.5	Sheep, rabbits	1 m high in 1978	Yes
4	9	Moolpa Station	YG478325	41	0.06	Cleared 1972, last cropped 1976, very light stock grazing since	1977	Yes
	10	Moolpa Station	YG482332	58	0.05	Cleared 1977, last cropped 1980, very light sheep grazing since	1981	Yes

Table 1. General characteristics of the study sites including details of *Acacia melvillei* regeneration. Grid references are from 1:100,000 topographic maps or orthophotomaps.

Weeks since planting	Observation date (1991)	Caged				Uncaged			
		Live	Dead-browsed	Dead-unbrowsed	Disappeared	Live	Dead-browsed	Dead-unbrowsed	Disappeared
(a) First planting									
6	25 June	69	0	31	0	31	29	40	0
12	7 Aug	69	0	31	0	23	37	40	0
18	11 Sept	52	0	46	2	8	44	46	2
(b) Second planting									
6	7 Aug	100	0	0	0	94	4	2	0
12	11 Sept	83	0	15	2	59	27	12	2
(c) Third planting									
6	11 Sept	75	0	25	0	38	33	29	0
Percentage over all plantings on 11 Sep		70	0	29	1	35	35	29	1

Table 2. Survival and causes of death (as percentages) for seedlings of *Acacia melvillei* planted on three dates inside and outside cages. Percentages are based on n = 48.
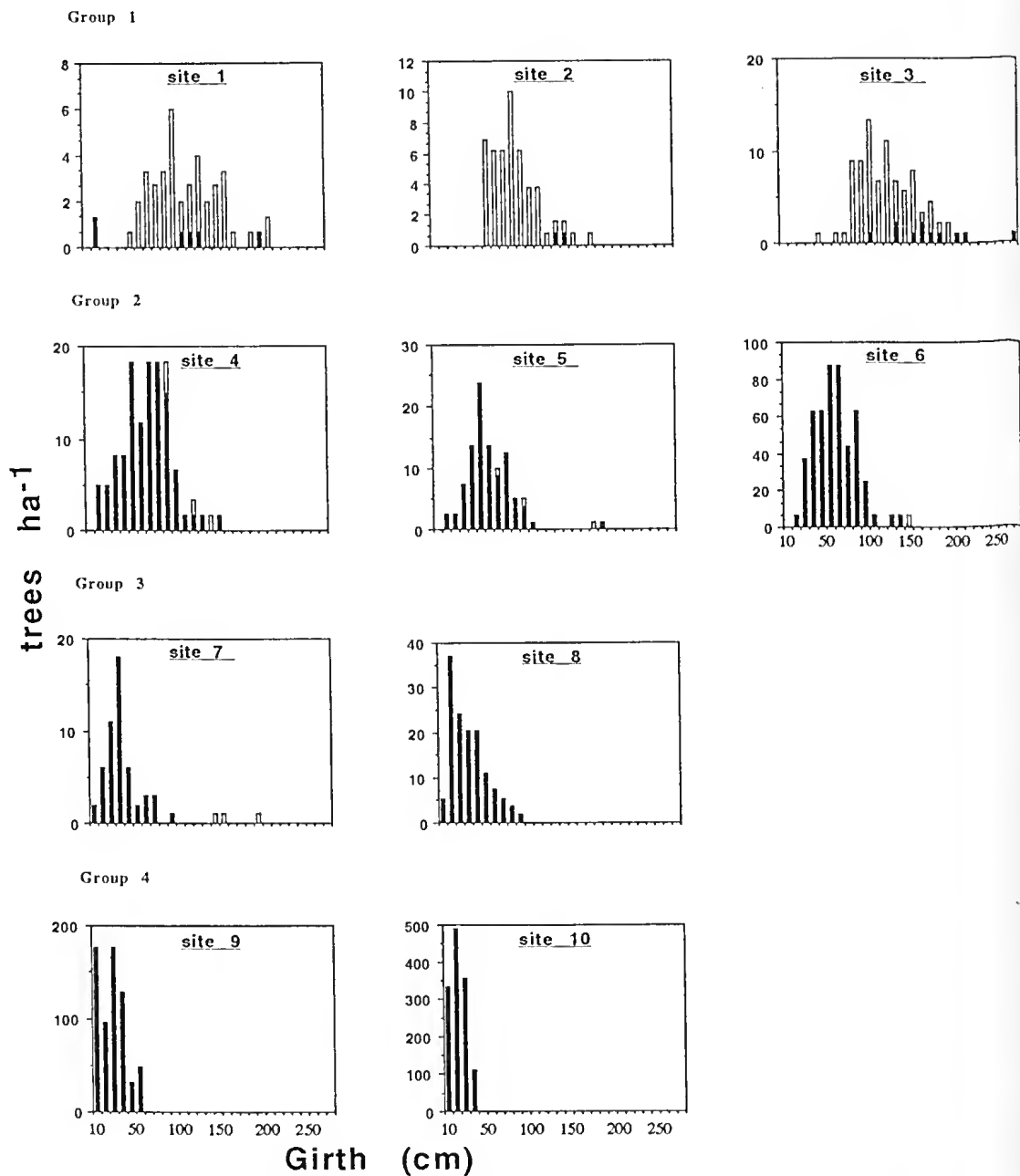
Fig. 2. Girth histograms for stands of *Acacia melvillei* divided into groups of similar size structure. Shading shows live plants, no shading shows dead ones. Vertical scale varies.

Although some of the few live plants in group one have similar girths to plants in group two, their dead branches and sparse canopy make them readily distinguishable from group two plants with their dense eanopies and strongly suggest that they are from an earlier episode of regeneration.

Stands in groups two and three are mostly of living plants (Fig. 3B, C). While group three has a few plants in the smallest size elass, the few that are less than 1 m high have been suppressed by browsing. In both groups there is a laek of reeent reeruitment (Fig. 2). In any given stand, most plants appear to be of similar age and possibly from a single reeruitment event, with the group two stands being older than those of group three. Group two plants typieally have eanopies wider in relation to their height than group one plants (Fig. 3B,C). There were a few dead or degenerating trees at eaeh site, including site 8 where, however, they were absent from the quadrat. Exeavation of small plants at each site showed they were of seedling origin in every ease.

Taken together the group two data (Fig. 2, Table 1) suggest that group two sites earry substantial regeneration from the early 1950s. Site four was exelosed from stock in 1952 but rabbits periodieally infest the area between control measures sueh as ripping (R. Seriven personal eommunieation), and there have been episodes of stoek entry (Semple 1986). Regeneration eommeneed in 1952–1953 soon after exelosure (Soil Conservation Serviee, Hay, unpublished records). Of groups two, three and four, this site shows the greatest range in sizes of *A. melvillei*, from plants 1 m tall to large, degenerating trees. It may well be an exeeption to a possible general trend to even-aged stands in these three groups. On the same soil type outside the exelosure, *Acacia melvillei* regeneration was absent; only dead (the great majority) or very degenerate plants oeeurred (see also Semple 1987).

Further evidenee linking group two to the 1950s is an eyewitness report that the present live plants at site 5 first appeared in the early 1950s (Gordon Neil personal eommunieation). This would aeeord with regeneration episodes of other speeies in the 1950s during above-average rainfall years and myxomatosis-induced reduetion in rabbit numbers at that time (Hall et al. 1964, Chesterfield & Parsons 1985). At Balranald, 1952, 1954, 1955, 1956 and 1958 had above-average rainfall. For group three the only dating we have is that the live plants at site 8 were about 1 m high when seen in 1978 (Greg Ayson personal eommunieation). The live plants at sites 7 and 8 could well relate to exceptionally wet years in 1973–1975, as do similar episodes in nearby areas (Chesterfield & Parsons 1985).

The group 4 sites are on areas that had been eultivated and used for eereal erops in the 1970s. When eropping stopped, profuse regeneration beeame obvious (Fig. 3D), mainly from root suekering but oeeasionally from seed (Fig. 4). The size elass differenee between sites 9 and 10 (Fig. 2) aeeords well with their known history (Table 1). The site 9 histogram is bimodal (Fig. 2), with the 0–10 em peak indicating a younger generation of root suekers, possibly a response to root damage around the base of the trees eaused by cattle hooves. Mieroseopie examination of transverse sections eonfirmed that the suckers at sites 9 and 10 originated from roots, not rhizomes.

Seedling survival

Of untreated seeds set out to germinate at 25°C, only 10% germinated; the proportion was inereased to 95% by placing seeds in boiling water or by nieking the seed eoat. As expected, rainfall was lowest and temperatures highest for the first and last six weeks of the trial (Fig. 5). The first planting in mid-May was made in dry eonditions after below-average autumn rainfall. Winter rainfall was slightly above average.

On all three observation dates after the first planting, overall seedling mortality was higher in uneaged plots than in eaged ones (Table 2). No dead-browsed seedlings were found in eages so invertebrate effeets were not detected. The only signs of vertebrates were rabbit seats and rabbits whieh are assumed responsible for all browsing deaths. After six weeks in uneaged plots, browsing mortality varied signifieantly ($P < 0.001$) between planting dates, with smaller losses in the moist, eool winter period when fresh, green herbs were abundant as an alternative food source.

The deaths of unbrowsed seedlings were not related to transplanting damage. Mortality was greatest during the dry periods of May–June and August–September and was very low in the moist seeond six weeks of the trial when it was mueh less than browsing losses (Table 2). The data strongly suggest that the deaths of unbrowsed seedlings were due almost entirely to drought and that frost was unimportant. In 1991, only 12 frosts were reeorded at Swan Hill eompared to an average of 19 and sereen temperatures never fell below 0°C (Australia:

Fig. 3. *Acacia melvillei* stands in order of decreasing presumed age. A, dead and partly dead plants up to 5 m high at site 3. B, plants up to 4 m high, site 5. C, plants up to 3 m high, site 8. D, plants (mostly root suckers) up to 2 m high in paddock last cultivated in 1980, site 10. Scale in A, B and C is 1.4 m high.

Fig. 4. Three *Acacia melvillei* sucker shoots arising from swollen part of horizontal root following mechanical disturbance on roadside, Sturt Highway 41 km west of Balranald. Sheet of paper is 21 cm wide.

Bureau of Meteorology unpublished data). Seedling density of species other than *A. melvillei* in the plots was too low to affect the mortality rates recorded.

On 30 November 1991 only 18 plants were alive, all in cages. This number fell to six by 25 March 1992, all in a single cage from the third planting. These plants were 2–3 cm high and had 4–6 leaves, the youngest having pinnate leaves attached to phyllodes. It is surprising that any plants survived their first summer given that

only 12.5 mm of rain fell in the Yarraby district between the above-average rains of September 1991 and the final inspection (J. A. McDowall personal communication). The six survivors comprise 4% of the seedlings planted in cages.

DISCUSSION

Size class analysis

The picture which emerged was of an almost total failure of *Acacia melvillei* regeneration throughout the pastoral part of the study area, with most stands seen being totally dead or with a great majority of dead trees. Similarly, of the seven arid zone *Acacia* species discussed by Auld (1990), only for *A. oswaldii* is there any chance that recruitment is sufficient to maintain current population densities.

The few exceptional sites showing some *A. melvillei* recruitment in the pastoral zone included an experimental exclosure, a home paddock, a public stock reserve and some other sites close to Balranald township with presumed intermittently low browsing pressure (the last sites were not sampled). The reasons why recruitment at some of these sites (sites 7 and 8) was not suppressed by browsing are unknown. Similarly, it
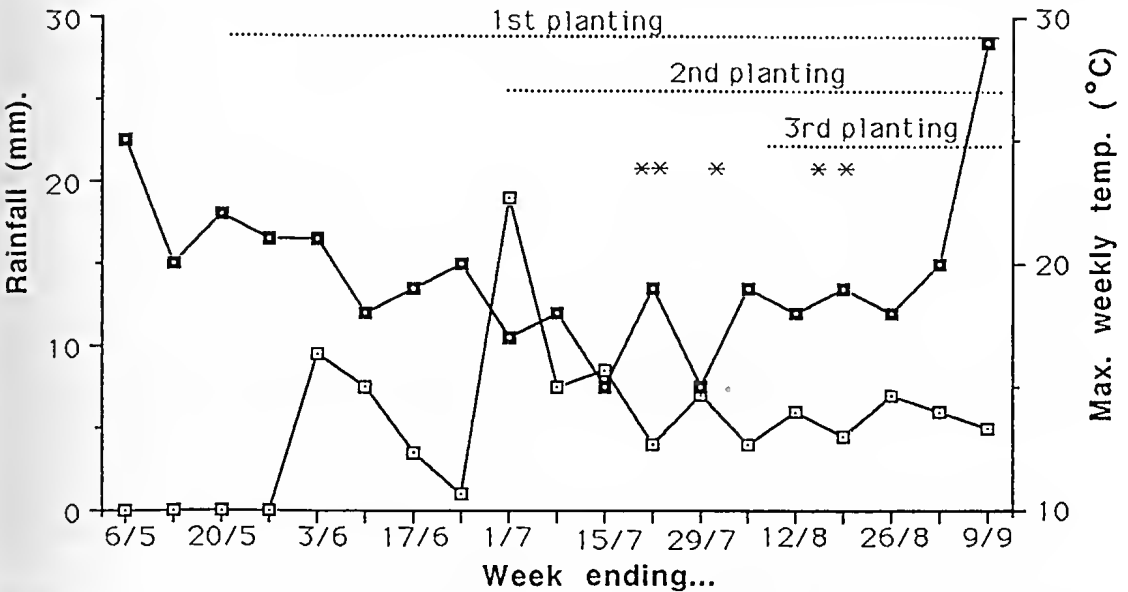
Fig. 5. Climatic data and timing of the plantings in the seedling survival trial at Flora Reserve G67. Closed squares = weekly rainfall; open squares = maximum temperature; asterisks = occurrence of frosts (from thermometer at site).

is not known why the two major recruitment episodes identified here in the pastoral zone in the last 50 years failed to occur at all the group two and three sites; relevant grazing histories are simply unavailable.

While landholders who produce profuse suckering of *A. melvillei* by cultivation regard it as a woody weed, suckers were only recorded after mechanical disturbance of roots, either in paddocks or along roadsides (Fig. 6). Thus, it seems that suckering has only been significant since introduction of European land use practices, as for *A. harpophylla* (Williams 1985). By contrast, *A. carnei* suckers independently of root disturbance, while *A. oswaldii* does not sucker at all (Auld 1990).
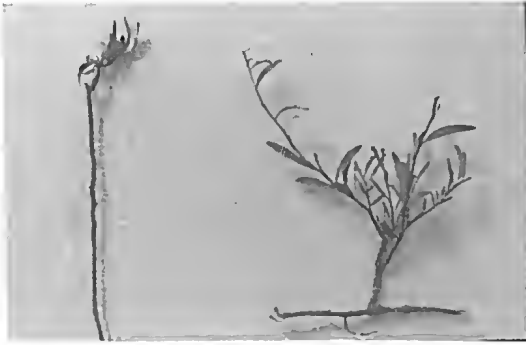
Fig. 6. Excavated *Acacia melvillei* specimens from sites 9 and 10 showing difference between plants originating from seedlings (left) and root suckers (right). Horizontal root is 14 cm long.

Seedling survival

The major factor limiting seedling establishment was low soil moisture, especially in spring and summer. Browsing by rabbits was also important. These findings also apply to *Acacia oswaldii* seedlings (Auld 1990) and to other species from semi-arid areas (Parsons 1968, Wellington 1989). While frost damage was not seen and mortalities did not seem to correlate with frosts, further work is needed on this given the unusually mild winter and evidence of frost deaths in other species (Parsons 1968).

Concluding discussion

It is clear from both size class analysis and the seedling survival study that, in the part of its range investigated, *Acacia melvillei* is subject to serious regeneration problems. Retaining this species in biological reserves is very likely to

require strict control of rabbit populations. The same applies to pastoral areas, along with stock removal during and after the rare high rainfall events likely to be needed for successful regeneration.

REFERENCES

Auld, T. D., 1990. Regeneration in populations of the arid zone plants *Acacia carnei* and *A. oswaldii*. *Proceedings of the Ecological Society of Australia* 16: 267–272.

Chesterfield, C. J. & Parsons, R. F., 1985. Regeneration of three tree species in arid southeastern Australia. *Australian Journal of Botany* 33: 715–732.

Condon, R. W., 1983. Pastoralism. In *What Future for Australia's Arid Lands?*, J. Messer & G. Mosley, eds, Australian Conservation Foundation, Melbourne, 54–60.

Crisp, M. D. & Lange, R. T., 1976. Age structure, distribution and survival under grazing of the arid-zone shrub *Acacia burkittii*. *Oikos* 27: 86–92.

Dick, R. S., 1975. A map of the climates of Australia according to Köppen's principles of definition. *Queensland Geographical Journal* 3: 33–69.

Fritts, H. C., 1969. Bristlecone pine in the White Mountains of California. *Papers of the Laboratory of Tree-Ring Research* 4: 1–44.

Hall, E. A. A., Specht, R. L. & Eardley, C. M., 1964. Regeneration of the vegetation on Koonamore Vegetation Reserve, 1926–1962. *Australian Journal of Botany* 12: 205–264.

New South Wales: Soil Conservation Service, 1990. *Hay District Technical Manual*. Soil Conservation Service, Sydney.

Parsons, R. F., 1968. An introduction to the regeneration of mallee eucalypts. *Proceedings of the Royal Society of Victoria* 81: 59–68.

Parsons, R. F., 1990. Plant conservation problems at species level in Mallee lands. In *The Mallee Lands: a Conservation Perspective*, J. C. Noble, P. J. Joss & G. K. Jones, eds, CSIRO, Melbourne, 25–28.

Pedley, L., 1978. A revision of *Acacia* Mill. in Queensland. *Austrobaileya* 1: 75–234.

Semple, W. S., 1986. Plant species lists from four exclosure sites in the Hay district of south-western

New South Wales. *Cunninghamia* 1: 491–502.

SEMPLE, W. S., 1987. Prior streams and Queel Queel Gums—regeneration areas revisited. *Journal of Soil Conservation New South Wales* 43: 38–43.

WELLINGTON, A. B., 1989. Seedling regeneration and the population dynamics of eucalypts. In *Medi-terranean Landscapes in Australia*, J. C. Noble & R. A. Bradstock, eds, CSIRO, Melbourne, 155–167.

WILLIAMS, O. B., 1985. Population dynamics of Australian plant communities, with special reference to the invasion of neophytes. In *The Population Structure of Vegetation*, J. White, ed., Junk, Dordrecht, 623–635.

PROFESSOR JOHN TURNER

Professor John Turner, OBE (1974), MA, PhD, (Cantab.), LLD (Melb. Hon.), FAA was Professor of Botany at Melbourne University from 1938 to 1973. During that period he was a member and later a councillor of the Royal Society of Victoria. He was president from 1951 to 1952.

Professor Turner was born in Yorkshire in 1908, son of T. S. Turner, and was educated at Sheffield Central School and at Cambridge University. He came to Melbourne in 1938 as a young man from Cambridge where he was Senior Demonstrator and where he had made a significant contribution to research on the physiology of tissue respiration, pioneering the use of the Warburg manometer. He arrived in a drought year and experienced the dreadful bush fires that swept through Victoria in January 1939. During the Second World War Professors Turner and Hartung established an optical laboratory in the Botany School where optical instruments intended for the tropics were proofed with fungicide to prevent mould.

Throughout his 35 years as head of the department, Professor Turner taught students from first year biology to final year. He led a group of research students in plant physiology. In 1952 he was elected as a corresponding member of the American Society of Plant Physiologists, and in 1956 he was made a Fellow of the Australian Academy of Science in recognition of his research in plant physiology. He served on the Council of the Academy from 1967 to 1970.

Recognising the need for a modern ecological approach to land management, Professor Turner organised the Academy's ecological research in the Kosciusko National Park. He also headed a team of ecologists in research on the flora of the Victorian High Plains. The whole department was involved in this ecological venture, and we all owe much to his inspired leadership and stimulating company. One of his major achievements was to establish the field laboratory and bunkhouse at Wilsons Promontory as a centre for student excursions and research projects. His love of field work emanated from student days on the Yorkshire and Derbyshire moors.

During the last 50 years Professor Turner made a lasting contribution to the conservation of the Australian landscape and flora. He had both national and international standing and was author of definitive reports based on scientific evidence for areas such as Norfolk Island (for the Australian Conservation Foundation). His work with the "Save the Dandenongs League" prevented over-commercialisation of the Dandenong Ranges and resulted in a scenic bush park with superb views of mountain, forest and water. He worked to save roadside trees in the Dandenongs, in Hawthorn and on St Kilda Road.

Professor Turner was a foundation member of the National Trust, the Australian Conservation Foundation, the Victorian National Parks Association (president 1969–1973), and the Land Conservation Council (member 1970–1979). His positive clear thinking underlies the principles which form the bases of these organisations. He was chairman of the Maud Gibson Trust which funded the preparation and publication of *The Handbook to Plants in Victoria* by James Willis, and the formation of the Royal Botanic Gardens Annexe at Cranbourne, 330 ha for the growing of Australian native species. While councillor and president of the Victorian National Parks Association, Professor Turner supervised and edited their first major publication, *Nature Conservation in Victoria* by Judith Frankenberg.

As an educationalist Professor Turner had a major impact on school General Science, ensuring that students in years 9 and 10 received a broad science basis instead of selecting from four individual science subjects. He was co-author of a general science text in 1943. Subsequently he revolutionised biology teaching for years 11 and 12 by co-operating with David Morgan to produce *The Web of Life*. He was chairman of the Board of Forestry Education for nearly 20 years, and helped to achieve integration of Forestry at Creswick and at the University of Melbourne. Professor Turner was Dean of Science in 1968 and served on the University Council for many years.

Professor Turner appreciated landscapes both as an ecologist and as an artist, in drawings, watercolours, linocuts, scrapeboard and later in lithographs. He was President of the National Gallery Society of Victoria.

As a person Professor Turner mastered the art of conversation. Humour, wit and a fund of good yarns made him the very antithesis of the mono-cultural stereotype immortalised by C. P. Snow. Many an evening has been brightened by his light-hearted verse. His love of plants, of gardens and of the bush, shows through all his interests. He retired to Castlemaine where he died on 5 May 1991. He is survived by his wife, Kaye, his children, Susan and Peter, and four grandsons.

GRETNA WESTE
Botany School
University of Melbourne
Parkville, Victoria 3052

PROCEEDINGS

OF THE

ROYAL SOCIETY OF VICTORIA

Volume 105

1993

CONTENTS OF VOLUME 105

STUDIES ON WESTERN AUSTRALIAN PERMIAN BRACHIOPODS 11. NEW GENERA, SPECIES AND RECORDS

N. W. Archbold

School of Aquatic Science and Natural Resources Management, Deakin University, Rusden Campus, 662 Blackburn Road, Clayton, Victoria 3168

Archbold, N. W., 1993:03:31. Studies on Western Australian Permian brachiopods 11. New genera, species and records. *Proceedings of the Royal Society of Victoria* 105 (1): 1–29. ISSN 0035-9211.

New genera, species and records of Permian Brachiopoda that are important in the biostratigraphy of the Western Australian Permian marine sequences are described and illustrated. New taxa described include *Gatia superba* gen. et sp. nov., *Heteralosia (Etherilosia)* subgen. nov. (type species *Strophalosia etheridgei* Prendergast, 1943), *Coolkilella* gen. nov. (type species *Cancrinella coolkilyaensis* Archbold, 1983), *Neochonetes (Sommeriella) nalbiaensis* sp. nov., *N. (S.) hardmani* sp. nov., *Costatumulus occidentalis* sp. nov., *Cartorhium imperfectum* sp. nov. and *Spirelytha kashirtsevi* sp. nov. A lectotype is designated for *Productus humboldtii* d'Orbigny, 1842, type species of *Waagenoconcha* Chao, 1927.

SINCE the publication of the first ten parts of this series of works on Western Australian Permian brachiopods, numerous additional specimens have been collected by various organisations or have been found in institutional collections. The present study brings together various specimens that add to new generic concepts, represent new species or new records of stratigraphical occurrences, or provide new morphological information.

The specimens described come from the Permian sequences of the Perth, Carnarvon, Canning and Bonaparte Gulf Basins of Western Australia. References to the Permian stratigraphy of these basins are given in previous parts of this series, and specific locality and stratigraphical data are given herein with the systematic descriptions. Each species is assigned to the Western Australian Permian brachiopod zonation recently proposed by me (Archbold in press).

All material described is deposited in the following institutions: the Australian Museum, Sydney (AMF); the Commonwealth Palaeontological Collections (CPC) of the Australian Geological Survey Organisation (AGSO), Canberra; the Geological Survey of Western Australia, Perth (GSWA F); the Department of Geology, University of Western Australia, Perth (UWA); the Western Australian Museum, Perth (WAM) and the Museum of Victoria, Melbourne (NMV).

All illustrated specimens of new species other than holotypes are paratypes.

SYSTEMATIC PALAEONTOLOGY

Phylum Brachiopoda
Order Strophomenida Öpik, 1934
Suborder Orthotetidina Waagen, 1884
Superfamily Orthotetacea Waagen, 1884
Family Derbyiidae Stehli, 1954
Subfamily Derbyiinae Stehli, 1954

Genus Derbyia Waagen, 1884

Type species. Derbyia regularis Waagen, 1884.
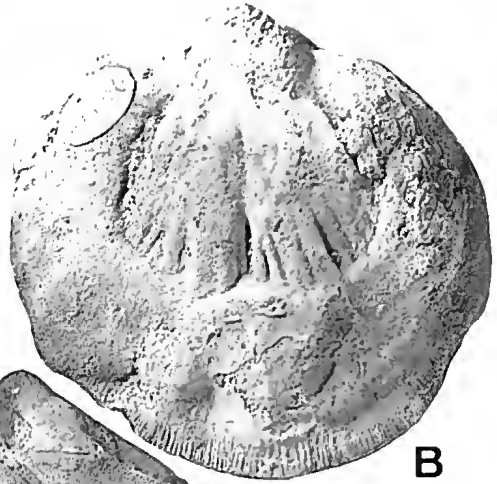
Derbyia hardmani Thomas, 1958a

Fig. 1A

Derbyia sp.—Thomas 1957: 181.—Thomas 1958b: 3.
Derbyia hardmani Thomas 1958a: 78, pl. 5, figs 5–9, pl. 18, fig. 6, pl. 9, fig. 2.—Thomas 1969: 221.—Archbold 1988a: 22.

Comments. This species has been recorded but never figured from the Upper Marine Beds of the Port Keats Group (Thomas 1957, 1958b; Archbold 1988a). The only available specimen (CPC 24511) comes from locality PK 4 (see map in Thomas 1957: 176), on the coast 13.5 km north of Cape Dombey, Port Keats area, Northern Territory. It is a large ventral valve (73 mm wide, 54+ mm length), essentially flat with a gently concave median portion and strongly convex posterior lateral flanks. Although it is preserved as a natural ferruginous cast, traces of fine costellae, some 10 to 11 per 5 mm at 3 to 4 cm from the umbo, are visible. Costellae in-
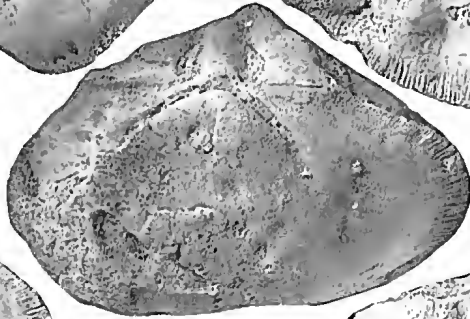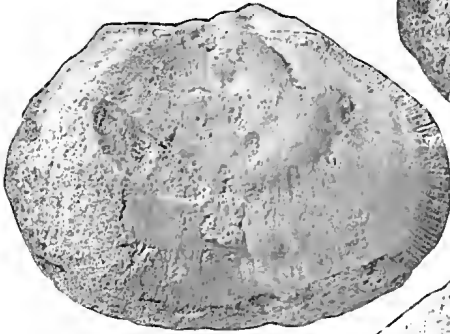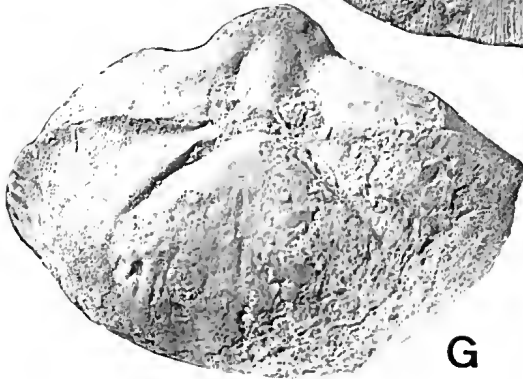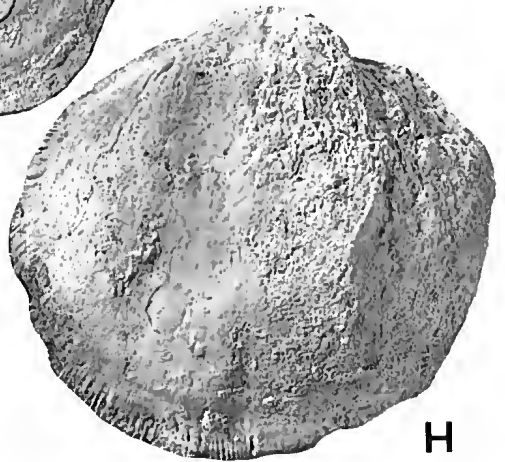
Fig. 1. A, *Derbyia hardmani* Thomas, CPC 24511, natural east of ventral valve, × 1. B–H, *Streptorhynchus luluigui* Hosking. B, G, H, AMF 45006, complete internal mould of shell in ventral, posterior and dorsal views, × 1. C, D, F, AMF 44980, internal mould of shell in posterodorsal, dorsal and ventral views, × 1. E, AMF 44974, internal mould of shell in ventral view, × 1.

erease by intercalation. The poorly preserved interarea is low (approximately 9 mm high), flat and apsacline.

Zone. Waagenoconcha imperfecta Zone. Dzhulfian.

Family STREPTORHYNCHIDAE Stehli, 1954

Genus Streptorhynchus King, 1850

Type species. Terebratulites pelargonatus Schlotheim 1816.

Streptorhynchus luluigui Hosking, 1932

Figs 1B–H, 2A–C

Streptorhynchus luluigui.—Arehbold 1988a: 24, fig. 2A–Q (with synonymy).

Comments. This species has been extensively described and figured from the Hardman For-

mation of the Canning Basin (Hosking 1932, Thomas 1958a), where it appears to be restricted to the Kirkby Range Member (Arehbold 1988a). In the Bonaparte Gulf Basin sequence, *S. luluigui* is characteristic of Assemblage C of Thomas (1957, 1958b) and is apparently absent from Assemblage D (Arehbold 1988a).

No specimens have been figured previously from the Upper Marine Beds of the Port Keats Group, Bonaparte Gulf Basin, despite a magnificent suite of material having been collected by H. O. Fletcher of the Australian Museum in 1952 from an ironstone ridge at the Port Keats Mission (locality 5 of Thomas 1957: 176). A number of these specimens are figured herein because they are of relatively large size and, being internal moulds, show the muscle scars and the degree to which the external ornament is visible on the mature shell interior. Ventral musculature can be deeply impressed, as noted by Thomas (1958a). The ventral muscle field is
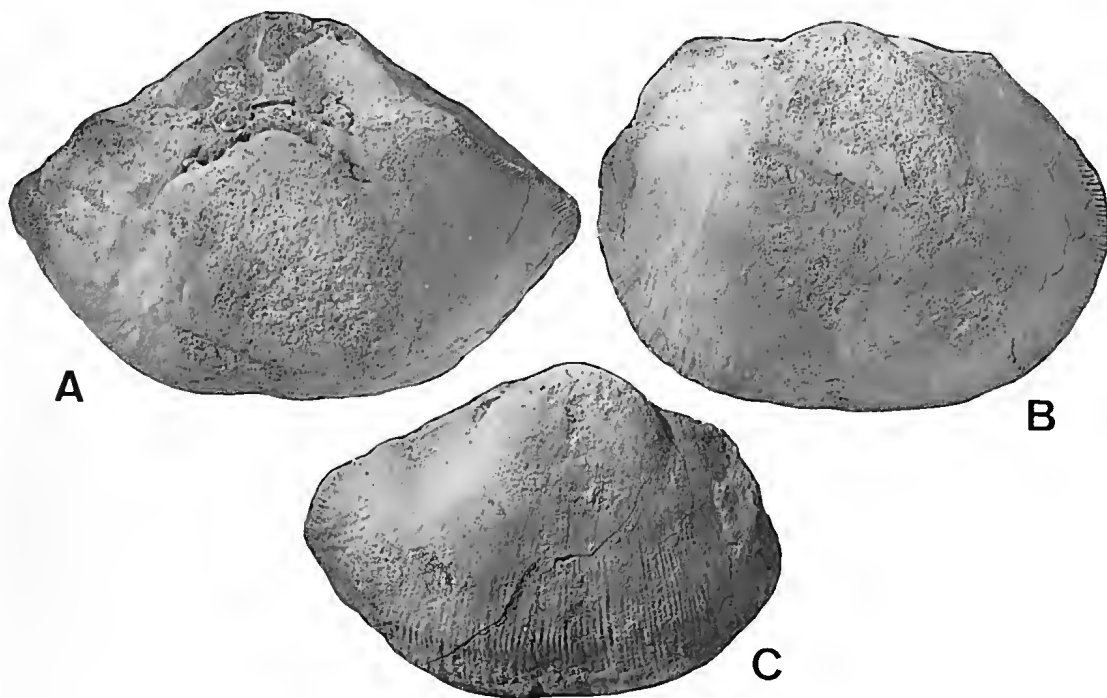

Fig. 2. Streptorhynchus luluigui Hosking. A, B, AMF 44996, internal mould of shell in posterior and dorsal views, × 1.2 and × 1. C, AMF 44974, internal mould of shell in dorsal view, × 1.

weakly divided by a low median ridge (Fig. 1B, E) at full maturity.

Zone. Liveringia magnifica Zone. Late Midian or Early Djhulfian.

Order CHONETIDA Nalivkin, 1979
Suborder CHONETIDINA Muir-Wood, 1955
Superfamily ANOPLIACEA Muir-Wood, 1962
Family ANOPLIIDAE Muir-Wood, 1962

Genus **Gatia** gen. nov.

Etymology. For Dr G. A. Thomas, palaeontologist and stratigrapher.

Type species. Gatia superba sp. nov.

Diagnosis. Large, smooth anopliid-shaped shells, widest at hinge. Ventral interior with short median septum posteriorly and with parallel vascular trunks extending to valve anterior on either side of septum. Dorsal interior with short lateral septa extending to form rounded, club-shaped brachiophores. Short median septum arising anterior to shallow alveolus and separated from short central septum by narrow depressed region. Short accessory septa (or ridges) developed anterior to central septum, apparently by fusion of a row of papillae.

Discussion. The dorsal interior of *Gatia* gen. nov. resembles that of no other anopliid genus. The short accessory septa (or ridges) suggest an anopliid affinity but the central septum, anterior to the short median septum, recalls ontogenentic stages of rugosochonetids. Lateral septa also recall rugosochonetids. Nevertheless, the advanced brachial ridges of Permian rugosochonetids are absent. The subfamilial position of *Gatia* is left open; the genus would probably fit within the Anopliinae in the sense of Archbold (1980a) but it is not clear where it would be placed in the scheme proposed by Afanasycva (1988).

Gatia superba sp. nov.

Fig. 3A–L

Tornquistia magna Archbold 1980a (*partim*): 186, pl. 25, figs 9, 13 (*non cet.*).

Holotype. An isolated dorsal valve (NMV P120329) from the Lyndon River, 9.20 km (5.75 miles) west-north-west of Round Hill Well, Mia Mia Station, Carnarvon Basin; originally mapped as Bulgadoo Shale, now Madeline Formation, lower member. This and all other specimens (below) were presented to the Department of Geology, University of Melbourne by the Bureau of Mineral Resources on 8 Feb. 1954.

Other material. Paratypes: NMV P120330, an isolated dorsal valve; NMV P120331–P120333, three conjoined shells; and NMV P120334–P120336, three isolated ventral valves. Forty-three additional specimens were available for study. All specimens are from the same collection as the holotype.

Size ranges. Maximum width 11.9–16.4 mm; ventral length 9.2–11.3 mm; dorsal length 7.5–10.2 mm.

Description. Large sized anopliid. Convexity of ventral valve pronounced with strongly inflated mesial portion in the form of a broad fold. Dorsal valve concave with marked median concavity corresponding with broad ventral fold. Greatest width of shell at hinge line. Exterior surface of shell smooth with few growth lines, except for anterior of mature valves where growth lines are more distinct and numerous. Ventral interarea prominent, about 1.5 times dorsal interarea height. Cardinal spines poorly preserved, widely spaced. Ventral umbo fine and rounded.

Ventral interior with prominent, large, strong teeth. Delthyrium distinct with thickening of shell beneath it. High, sharp median septum bisects delthyrium and extends short distance anteriorly on valve floor. Small, distinct pseudodeltidium in apex of delthyrium. Parallel vascular trunks arise adjacent to septum and extend anteriorly for most of valve length. Muscle scars weakly impressed. Anterior and lateral margins of valve interior finely papillose.

Cardinal process distinct, blunt; internal face weakly bilobed, exterior face quadrilobed. Distinct chilidium beneath exterior face of process. Valve interior with shallow alveolus at base of cardinal process. Short, broad median septum arises anterior to alveolus. Median septum truncated at anterior end by small depression, anterior to which arises a short central septum. Lateral septa short, broad and distinct, extending anteriorly to form rounded, club-shaped

Fig. 3. Gatia superba gen. et sp. nov. A, NMV P120330, isolated dorsal valve, interior view, × 3.5. B, C, NMV P120329, holotype, isolated dorsal valve, interior and exterior views, × 3.5. D, E, NMV P120331, shell in ventral and dorsal views, × 3.6. F, NMV P120334, isolated ventral valve, interior view, × 3.7. G, NMV P120332, shell in ventral view, × 3.6. H, NMV P120335, ventral valve interior view, × 3.6. I, NMV P12O336, ventral valve interior view, × 3.5. J–L, NMV P120333, shell in ventral and dorsal views, × 3.5, and umbonal region enlarged, × 5.
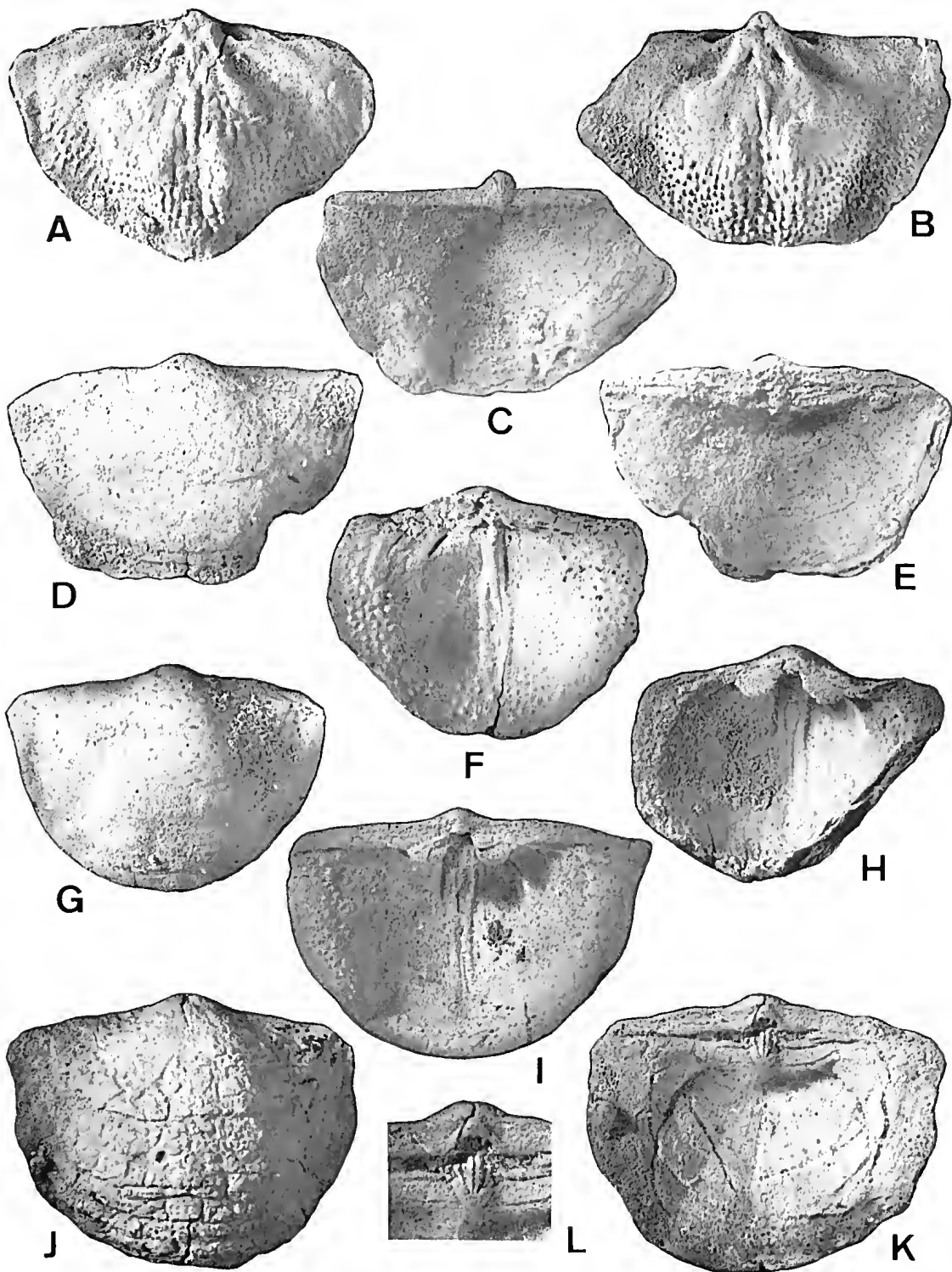
braehiophores. Soeket plates stout, soekets large. Anterior of valve with rows of radiating papillae; adjaeent and anterior to the central septum, two or more of these rows fuse to form rough, aecessory septa (or ridges). Posterior margins of valve smooth.

Discussion. No other speeies is known with the combination of large size and the dorsal internal features of *Gatia superba.* Other Western Australian anopliids deseribed by me (Archbold 1980a, 1990) exhibit ineipient eharacters of this new form, such as the minute lateral and median (eentral) septa, but in dorsal structures those speeies do not elosely resemble *Gatia superba.*

Two ventral valves from the lower member of the Madeline Formation were previously ineluded by me in *Tornquistia magna* (Archbold 1980a, pl. 25, figs 9a, b, 13a–e). They are large valves that are morphologieally similar to the present population. Henee *Tornquistia magna* is now eonsidered to be restrieted to the true Bulgadoo Shale.

Zone. Echinalosia prideri Zone. Early Baigendzhinian.

Superfamily CHONETACEA Bronn, 1862
Family RUGOSOCHONETIDAE Muir-Wood, 1962
Subfamily RUGOSOCHONETINAE Muir-Wood, 1962

Genus Neochonetes Muir-Wood, 1962
Subgenus Neochonetes (Sommeriella) Arehbold, 1982

Type species. Chonetes prattii Davidson, 1859.

Neochonetes (Sommeriella) nalbiaensis sp. nov.

Fig. 4A–N

Neochonetes (Sommeria) tenuicapillatus Archbold 1981d (*partim*): 122, fig. 9X, Y (*non cet.*).

Holotype. A natural internal mould of a dorsal valve (GSWA F43854) from GSWA ficld loeality 9568 (photo reference Kennedy Range Run 2 Photo 5022), north-west of Paddy's Outeamp and south-west of Middalya Homestead, Carnarvon Basin; Nalbia Sandstone. Collector Dr S. K. Skwarko, June 1985.

Other material. Paratypes: GSWA F43855–F43857, three external moulds of ventral valves; GSWA F43858–F43861, four internal moulds of ventral valves; GSWA F43862, an external mould of a dorsal valve; GSWA F43863–F43867, five internal moulds of dorsal valves. Same loeality, horizon and colleetor as holotype.

Size ranges. Maximum width 12.2+–28.3 mm; hinge width 15.5–26.9 mm; height of ventral valve 11.8–18.2 mm; height of dorsal valve 8.2–19.1 mm.

Description. Large *Neochonetes.* Convexity of ventral valve gentle with shallow suleus arising close to umbo. Dorsal valve planar to gently eoneave with narrow, weakly developed fold developed anteriorly at maturity. Greatest width of shell at about mid-length or anterior to midlength. Exterior surfaee of shell with weakly developed growth lines and fine eapillae (about 4 per mm at 10 mm from umbo). Ventral interarea low, dorsal interarea very low. Cardinal spines projeet at variable angle (35° to 50°) on the one available speeimen. Ventral umbo low, rounded.

Ventral interior with short, stout teeth. Delthyrium distinet, broad, relatively small. Median septum arises under delthyrium, extends anteriorly for over three-quarters of valve length. Musele scars variably impressed; adductor sears usually indistinet, diduetor sears relatively distinet. Vaseular trunks weakly developed. Anterior and lateral margins of interior strongly papillose.

Cardinal proeess low, poorly known. Chilidium not known. Valve interior with prominent alveolus at base of proeess. Soeket ridges prominent; soekets distinet, deep. Lateral septa and median septum distinet, arising anterior to alveolus. Median septum extends anteriorly from 50% to 60% of valve length. Braehial ridges indistinet; region of ridges relatively eoarsely pa-

---

Fig. 4. *Neochonetes nalbiaeusis* sp. nov. A, GSWA F43855, latex cast of ventral valve external mould, × 2.5. B, GSWA F43858, latex cast of dorsal valve internal mould, × 1.7. C, GSWA F43863, latex cast of dorsal valve internal mould, × 3.2. D, GSWA F43862, latex cast of dorsal valve external mould, × 2.3. E, GSWA F43854, holotype, latex cast of dorsal valve internal mould, × 1.6. F, GSWA F43864, latex cast of dorsal valve internal mould, × 2.7. G, GSWA F43859, latex cast of ventral valve internal mould, × 2.5. H, GSWA F43865, latex cast of dorsal valve internal mould, × 2.3. I, GSWA F43856, latex cast of ventral valve external mould, × 2.3. J, GSWA F43860, latex cast of ventral valve internal mould, × 1.7. K, GSWA F43866, latex cast of dorsal valve internal mould, × 2.2. L, GSWA F43857, latex cast of ventral valve external mould, × 2.3. M, GSWA F43861, latex cast of ventral valve internal mould, × 2.1. N, GSWA F43867, latex cast of dorsal valve internal mould, × 2.1.
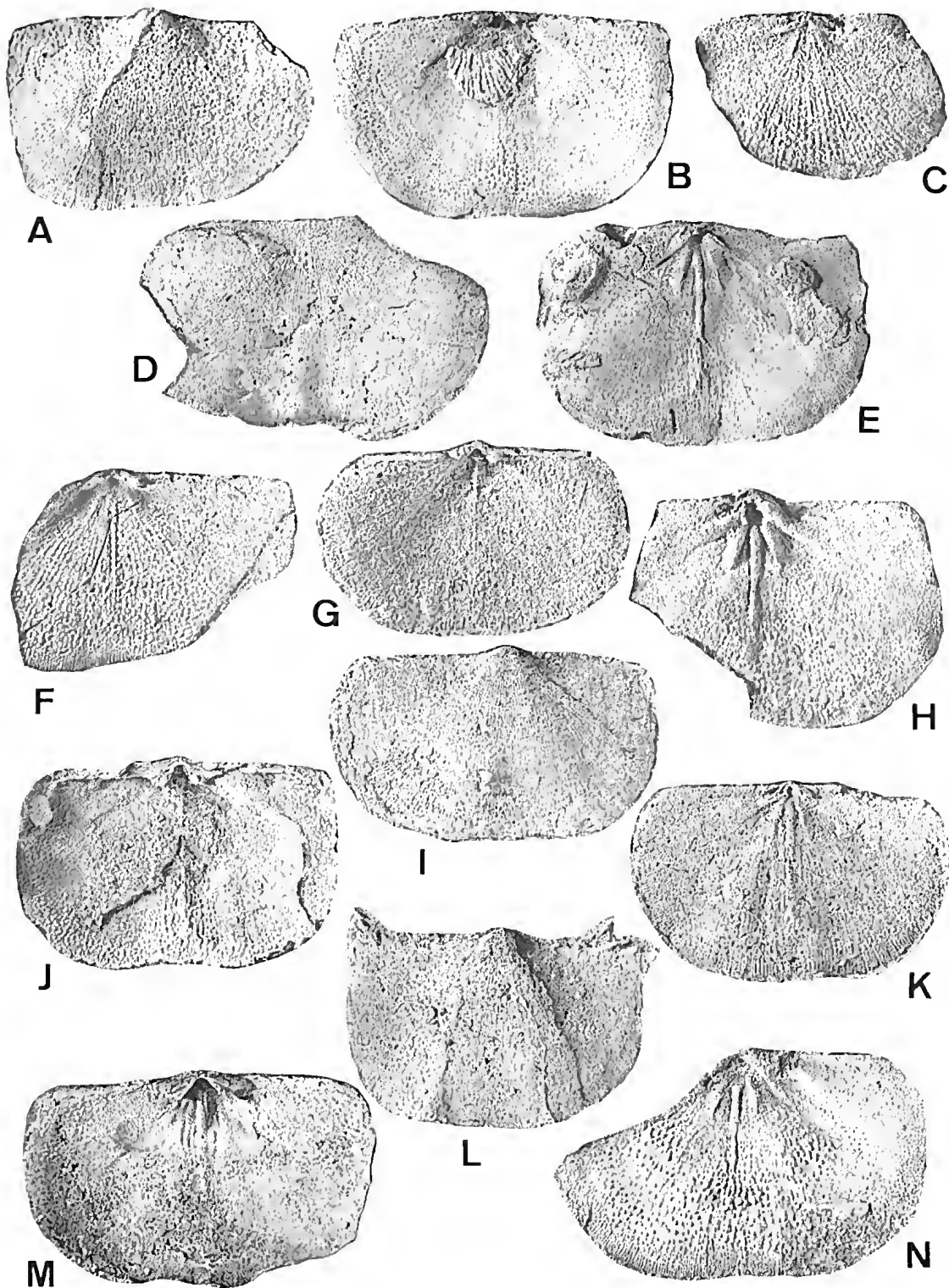
pillose at maturity. Anterior of dorsal interior with radiating rows of fine papillae. Posterior margins of valve smooth.

Discussion. This distinctive species requires well preserved collections to permit identification. The low ventral convexity and relatively flat dorsal valve discriminate the species from the slightly older *N. (S.) tenuicapillatus* Archbold, 1981d from the Upper Baigendzhinian of the Carnarvon Basin. The younger *N. (S.) afanasyevae* Archbold, 1981d also is characterized by low ventral convexity but the sulcus is even weaker in that species, the shell outline is somewhat rounder and the internal dorsal septa are more blade-like.

One submature shell from the Nalbia Sandstone was previously included by me in *N. (S.) tenuicapillatus* (see synonymy) but falls within the concept of the new species.

Zone. *Neochonetes (Sommeriella)* sp. nov. B zone of Archbold (in press), herein renamed the *N.(S.) nalbiaensis* Zone. Early Kungurian.

Neochonetes (Sommeriella) hardmani sp. nov.

Fig. 5A–O

Neochonetes (Sommeria) sp. A.—Archbold 1981d (*partim*): 126, fig. 12 A, B (*non* 12C).

Holotype. An isolated dorsal valve (NMV P120350) from a bed 1.25 m thick at about 40 m below top of Mount Hardman; Cherrabun Member, Hardman Formation, Canning Basin (same level as AGSO locality KLB 11), collector Dr G. A. Thomas.

Other material. Paratypes: NMV P120337–P120343, seven isolated ventral valves; NMV P120344, a conjoined shell; NMV P120345–P120349, five isolated dorsal valves; same locality and collector as holotype.

Size ranges. Maximum width 11.8–15.1 mm; hinge width 11.1–14.3 mm; height of ventral valve 9.2–11.0 mm; height of dorsal valve 7.7–10.2 mm.

Description. Small *Neochonetes.* Convexity of ventral valve distinct with shallow sulcus arising close to umbo. Posterior lateral margins of valve

clearly demarcated from remainder of valve. Dorsal valve planar with gently concave nepionic region. Dorsal fold obscure. Greatest width of shell usually at about 40% of shell length, rarely closer to mid-length. Exterior surface of shell with weakly developed growth lines and capillae (about 3 per mm at 5 mm from umbo). Ventral interarea low, dorsal interarea very low. Ventral umbo low, cardinal spines project at about 40° from posteror margin. Ventral teeth unthickened. Delthyrium distinct, broad. Median septum arises under delthyrium, extends anteriorly for 40% to 60% of shell length. Muscle scars usually weakly impressed. Parallel vascular trunks weakly to distinctly developed. Anterior and lateral margins of interior strongly papillose.

Cardinal process low, weakly bilobed on interior face, quadrilobed on exterior face. Chilidium not known. Prominent alveolus at base of process. Socket ridges stout, strong with deep slit-like sockets. Lateral septa present but not prominent. Median septum arises well anterior to the alveolus, blade-like and high anteriorly at maturity. Median septum extends anteriorly over 60% of valve length. Brachial ridges moderately distinct at maturity, developing and enlarging from radial rows of papillae. Anterior of dorsal interior with radiating rows of fine papillae. Posterior margins of valve interior smooth.

Discussion. Of all the Western Australian representatives of *Neochonetes (Sommeriella)*, only *N. (S.) hockingi* Archbold, 1991 resembles the present species in general shell dimensions. *N. (S.) hardmani* is readily distinguished from that species by its more prominent sulcus, demarcated posterior lateral margins, lower cardinal process and finer, more blade-like dorsal internal septa.

The large specimen of a ventral valve (CPC 1984; Archbold 1981, fig. 12C) is now excluded by me from *N. (S.) hardmani.* It apparently represents a larger, poorly known species that is probably allied to *Neochonetes (Sommeriella).*

Fig. 5. A–O, *Neochonetes (Sommeriella) hardmani* sp. nov. A, NMV P120337, ventral valve exterior view, × 3.2. B, K, NMV P120344, conjoined shell in ventral and dorsal views, × 3, × 3.2. C, NMV P120338, ventral valve exterior view, × 3.2. D, NMV P120339, ventral valve exterior view, × 3.2. E, NMV P120340, ventral valve interior view, × 3.2. F, NMV P120341, ventral valve interior view, × 3.2. G, NMV P120342, ventral valve interior view, × 3.2. H, NMV P120343, ventral valve interior view, × 3.2. I, NMV P120345, dorsal valve exterior view, × 3.2. J, NMV P120346, dorsal valve exterior view, × 3.2. L, NMV P120347, dorsal valve interior view, × 3.2. M, NMV P120348, dorsal valve interior view, × 3.2. N, NMV P120349, dorsal valve interior view, × 3.2. O, NMV P120350, holotype, dorsal valve interior view, × 3.2. P, Q, *Waagenites* sp., CPC 24512a, latex cast of ventral valve external mould, and CPC 24512b, ventral valve internal mould, × 3.5.
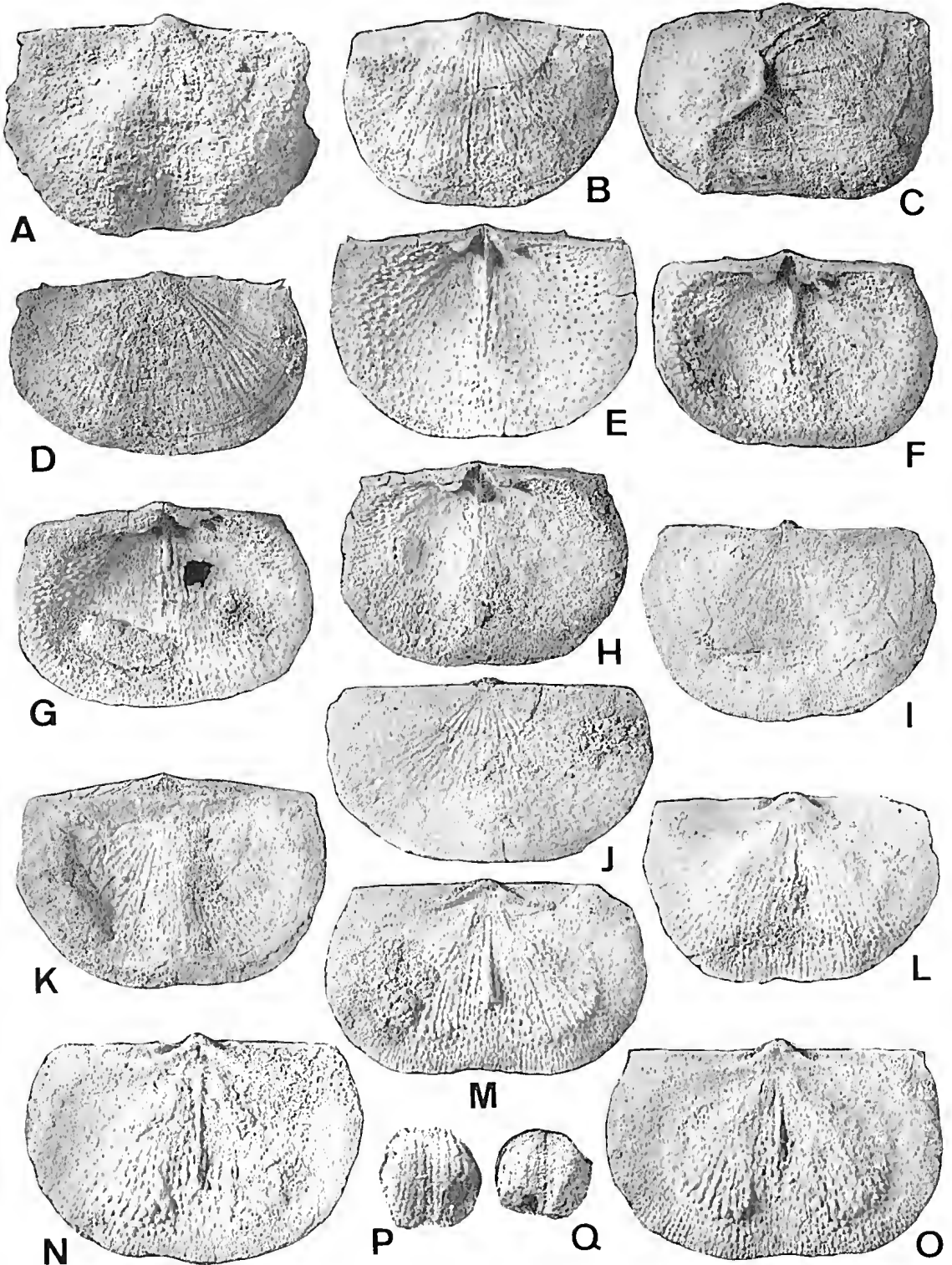
Neochonetes is not particularly common in Late Permian strata. Some species of this age show a trend towards weakly developed ornament and an obsolescent sulcus (Archbold 1981: 113). A few other species resemble *N. (S.) hardmani* in their stronger ornament, distinct sulcus and small size. Two such species are *Neochonetes pinegensis* (Kulikov, 1974) and *N. asseretoi* Fantini Sestini, 1964. *N. pinegensis*, from the Kazanian of the Pinega River, northern Russia, differs from *N. (S.) hardmani* in being widest at the hinge and in possessing a distinctive, concave dorsal valve (Likharev 1931, pl. 1, figs 15, 16, 20, 22, pl. 3, fig. 14). *N. pinegensis* has also been reported, with a query, from the Kazanian of the Kanin Peninsula (Stepanov et al. 1975: 57, pl. 1, figs 3, 4) but the material appears to represent a distinct species with strong sharp capillae and a narrow sulcus. *N. asseretoi*, from the Upper Ruteh Formation of Iran, differs from *N. (S.) hardmani* in possessing a more pronounced ventral umbo. *N. armenicus* Sokolskaya (in Ruzhentsev & Sarycheva 1965: 209, pl. 32, figs 1–3; see also Grunt et al. 1974: 130, pl. 58, figs 3–5) from the Djhulfian of Armenia is of comparable size to *N. (S.) hardmani* but lacks a sulcus and possesses a distinctly concave dorsal valve.

Zone. *Waagenoconcha imperfecta* Zone (Archbold 1988a). Djhulfian.

Genus **Waagenites** Paeckelmann, 1930

(= *Dienerella* Reed, 1931)

Type species. *Chonetes grandicosta* Waagen, 1884.

Waagenites sp.

Fig. 5P–Q

Waagenites sp.—Archbold 1988a: 22, 27.

Comments. A single specimen (CPC 24512a, b) of a small ventral valve (4.1 mm wide, 4.4 mm long), consisting of both the external and internal moulds, is figured herein. The specimen is from the Upper Marine Beds, Port Keats Group, at locality PK 4 on the coast approximately 13.5 km north of Cape Dombey, Port Keats area, Northern Territory.

The specimen is subquadrate in outline with a distinct sulcus and a short posteriorly located median septum. Costellae are prominent and increase by bifurcation. They number about 2 per mm, are broad, somewhat flattened and are separated by narrow, sharp troughs.

This species is readily distinguished from *Waagenites stani* Archbold, 1988, from slightly older strata in the Canning Basin, by means of its distinctive sulcus, shell outline and pattern of costellae. Although the specimen is inadequate for detailed comparison with other species of the genus, its small size, strong costellae and distinct sulcus strongly recall *Waagenites aequicosta* (Waagen, 1884, pl. 60, fig. 7a–c) from the Cephalopoda-bed of the upper *Productus* Limestone of Jabi (Pakistan), Salt Range.

Zone. *Waagenoconcha imperfecta* Zone. Djhulfian.

Subfamily Svalbardiinae Archbold, 1982c

Genus **Svalbardia** Barkhatova, 1970

Type species. *Chonetes capitolinus* Toula, 1875b.

Svalbardia narelliensis Archbold, 1981

Fig. 6A–J

Svalbardia thomasi Archbold, 1981b (*partim*): 6, fig. 2E, S, R (*non cet.*).
Svalbardia narelliensis Archbold 1981d: 11, fig. 2A–Y.

Comments. Two species of *Svalbardia* have been described from the Permian of Western Australia. *S. narelliensis* Archbold, 1981d from beds near the top of the Noonkanbah Formation, Canning Basin, invariably lacks a sulcus and usually possesses weakly developed dorsal internal structures. The slightly younger *S. thomasi* Archbold, 1981b possesses a more distinct sulcus at maturity and strongly developed dorsal internal structures. Other features of the two species are similar.

The present suite of figured specimens, GSWA F43859–F43868, collected by Dr S. K. Skwarko from the Nalbia Sandstone at the same locality as *Neochonetes (Sommeriella) nalbiaensis* (GSWA locality 69568), are referrable to *S. narelliensis*. The absence of a sulcus in all of the ventral valves is noteworthy, and brachial ridges are extremely feebly developed at maturity. Previously figured specimens from the Nalbia Sandstone (Archbold 1981, fig. 2E, S, R) are here referred to *S. narelliensis* and as a result *S. thomasi* is now considered to be restricted to the Baker Formation.

Zone. *Neochonetes (Sommeriella) nalbiaensis* Zone. Early Kungurian.

Order Productida Sarycheva & Sokolskaya, 1959

Suborder STROPHALOSIIDINA Waterhouse, 1975
Superfamily STROPHALOSIACEA Schuchert, 1913
Family STROPHALOSIIDAE Schuchert, 1913
Subfamily STROPHALOSIINAE Schuchert, 1913

Genus Heteralosia King, 1938
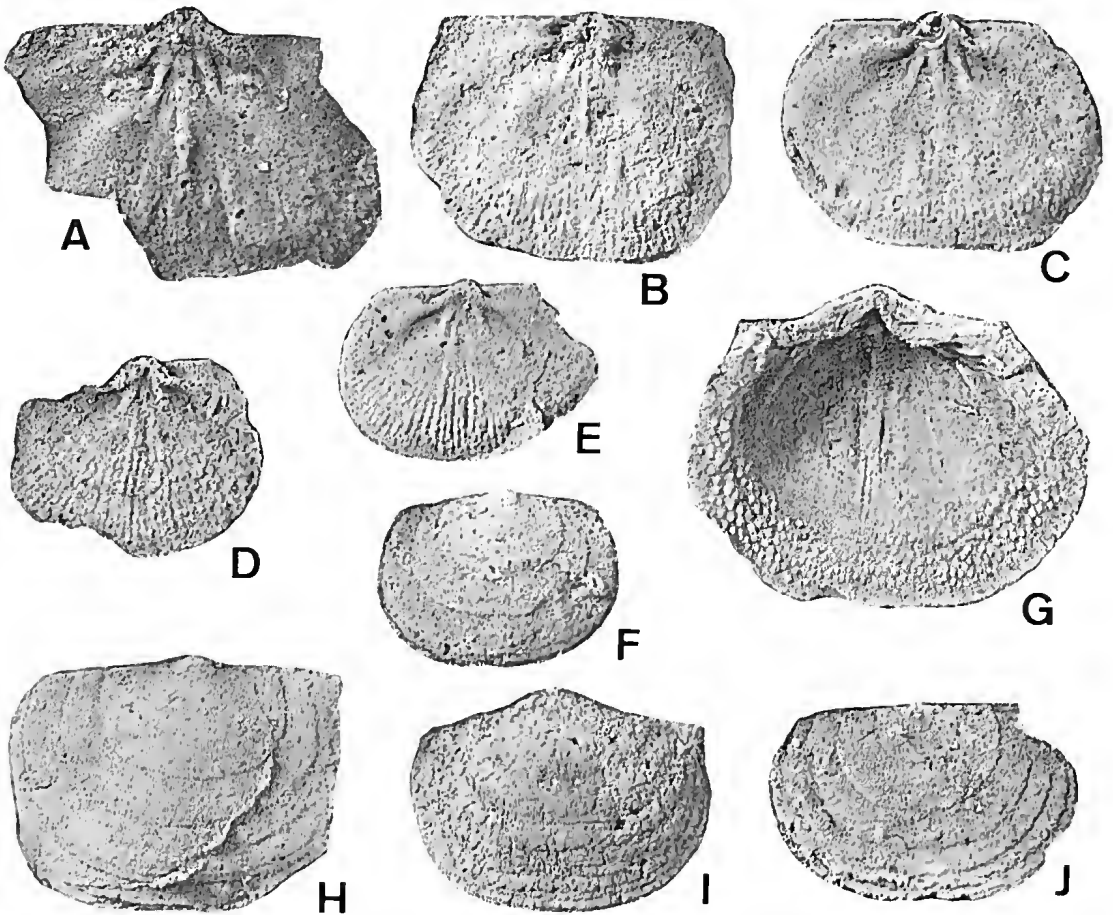
Type species. Heteralosia slocomi King, 1938.

Subgenus Heteralosia (Etherilosia) subgen. nov.

Type species. Strophalosia etheridgei Prendergast, 1943.

Etymology. For R. Etheridge Junior, 1847–1920.

Diagnosis. Small to medium sized *Heteralosia* species with distinct rhizoid spines of attachment, distinct relatively large cicatrix of attachment, and uniform suberect ventral spines.

Discussion. Heteralosia has previously been broadly interpreted by many authors including myself (Archbold 1986—see for review of previous literature). A re-examination of accounts of the type species by King (1938: 278, pl. 39, figs 15–18) and Muir-Wood & Cooper (1960: 80, pl. 3, figs 6–13) reveals some differences from Western Australian species previously re-

ventral valve external mould, × 3.5. G, GSWA F43865, latex east of mature ventral valve internal mould, × 3.2. H, GSWA F43866, latex east of ventral valve external mould, × 3. I, GSWA F43867, latex cast of ventral valve external mould, × 2.8. J, GSWA F43868, latex cast of dorsal valve external mould, × 3.2.

ferred to *Heteralosia*. These differences are con-
sidered to be of subgeneric importance and may
assist in delineating lineages of species within
Heteralosia.

Heteralosia (Etherilosia) lacks the two sets of
spines (erect and prostrate) distributed over the
entire ventral valve of *H. (Heteralosia)*, as de-
scribed by Muir-Wood & Cooper (1960: 81). *H.
(Etherilosia)* instead possesses uniform suberect
spines over the ventral valve. *H. (Etherilosia)* is
also characterised by a prominent cicatrix of at-
tachment accompanied by fine, rhizoid spines
which may attain a significant length in terms of
shell size (Archbold 1986: 106, 108, figs 3K, V,
4M). Rhizoid spines are not a feature of *H.
(Heteralosia) slocomi* (see Muir-Wood & Cooper
1960, pl. 3, figs 8–10).

The relatively large size of the cicatrix of at-
tachment of Western Australian species such as
H. (Etherilosia) etheridgei indicates that these
species remained attached throughout life, un-
like *H. (Heteralosia) slocomi*. It has been
demonstrated elsewhere (Archbold 1986) that
Western Australian species now referred to *H.
(Etherilosia)* are not juveniles of larger species.

Heteralosia (Etherilosia) prendergastae
(Coleman, 1957)

Fig. 7A–F

Comments. The revision of Western Australian
species of *Heteralosia* by Archbold (1986) re-
sulted in this species being restricted to one
specimen. A small collection of specimens from
AGSO Locality 7864 0142, described as "9 km
WNW of Wandagee Homestead, bank of Mini-
lya River, siltstone with mud clasts, probably
basal Cundlego Formation, Carnarvon Basin",
provides additional morphological data.

H. (E.) prendergastae is relatively large, up to
14.5 mm wide, with numerous semi-erect ven-
tral spines scattered over the valve. Rhizoid
spines are not well known but traces occur
around the cicatrix of attachment. Valve in-
teriors are typical of the genus.

The additional material appears to confirm
the suggestion (Archbold 1986) that *H. (E.) pren-
dergastae* is characterised by the possession of
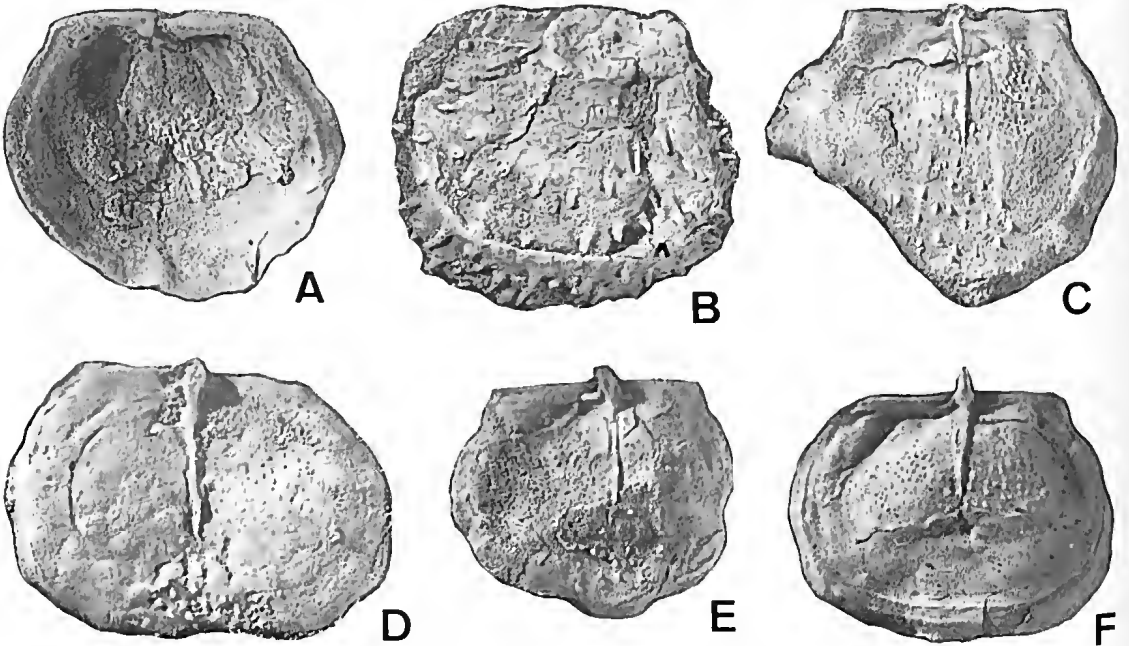relatively numerous ventral spines in compari-
son with other species.

Fig. 7. Heteralosia (Etherilosia) prendergastae (Coleman). A, CPC 24513, ventral valve interior, × 3.2. B, CPC
24514, ventral valve exterior view, × 3.0. C, CPC 24515, dorsal valve interior view, × 4.0. D, CPC 24516, dorsal
valve interior view, × 3.2. E, CPC 24517, dorsal valve interior view, × 3.2. F, CPC 24518, dorsal valve interior
view, × 3.2.

Measurements (in mm).

Specimen	Hinge width	Maximum width	Ventral height	Dorsal height
CPC 24513	9.4	12.9	11.4	—
CPC 24514	9.5	14.5	13.0	—
CPC 24515	7.3	10.6	—	10.1
CPC 24516	11.1	14.3	—	11.2
CPC 24517	7.6	9.8	—	8.7
CPC 24518	8.8	12.2	—	10.6

Zone. Fusispirifer cundlegoensis Zone. Late Baigendzhinian.

Genus **Wyndhamia** Booker, 1929

Type species. Wyndhamia dalwoodensis Booker, 1929.

Comments. Western Australian species of *Wyndhamia* were reviewed by Archbold (1987) who noted that further detailed description was required in order to understand the nature of the type species. *Arcticalosia* Waterhouse (1986a) may have use as a genus or subgenus when the ventral spine pattern of *Wyndhamia* is fully understood. Western Australian species referred herein to *Wyndhamia* possess ventral spines of uniform size, as in *Arcticalosia*, rather than of two sizes as stated to be the case in *Wyndhamia* (Waterhouse 1986a: 2).

For the present study, material of *Wyndhamia* species from the Carnarvon Basin, described originally by Coleman (1957), was reinvestigated and the specimens are refigured (Fig 8). Specimen locality data are provided by Coleman (1957). The review of Coleman's specimens indicates that three distinct species are present in the Late Artinskian and Early Kungurian faunas of the Carnarvon Basin. The earliest of these species, *Wyndhamia multispinifera* (Prendergast) from the Cundlego Formation, is characterised by fine, uniform ventral spines with short spine bases and a brush of fine spines over the ventral ears (Coleman 1957, pl. 18, figs 3, 4, 6, 7, 11, 12, 14 and probably 13; see also Archbold 1987, fig. 3G–K, P–Q, fig. 4A–F). Enlarged illustrations of ventral valve exteriors (Fig. 8B, K) confirm the nature of the fine spines and the short nature of most spine bases. The species is restricted to the *Fusispirifer cundlegoensis* Zone of Archbold (in press).

The second species, herein referred to as *Wyndhamia* sp. A, is based on limited material from the Wandagee Formation (Coleman 1957, pl. 18, figs 5, 8–10; also figured herein Fig. 8F, G, J, L). This species is distinguished by its

coarse ventral spines with relatively long spine bases (*W. colemani* Archbold, 1987 also possesses coarse ventral spines but lacks the long spine bases), distinctly convex dorsal interior (unlike that of *W. multispinifera* which is essentially flat), robust cardinal process (Coleman 1957, pl. 18, fig. 5) and distinct sulcus on the ventral valve. The species, occurring in the *Fusispirifer wandageensis* Zone of Archbold (in press), is not named because of the shortage of material.

The third species, herein referred to as *Wyndhamia* sp. B (see Archbold 1987, fig. 3L, M), is known only from a single incomplete dorsal valve from the Nalbia Sandstone (Early Kungurian). The flat nature of the dorsal interior suggests separation of the specimen from other known species of the genus. The species is restricted to the *Neochonetes (Sommeriella) nalbiaensis* Zone.

Suborder PRODUCTIDINA Waagen, 1883
Superfamily LINOPRODUCTACEA Stehli, 1954
Family LINOPRODUCTIDAE Stehli, 1954
Subfamily AURICULISPININAE Waterhouse, 1986b

Genus **Costatumulus** Waterhouse, 1983a

Type species. Auriculispina tumida Waterhouse in Waterhouse et al. 1983.

Comments. Cancrinella was interpreted broadly by me in an earlier study (Archbold 1983). Numerous generic names are now available in order to split lineages of species formerly attributed to *Cancrinella*. This splitting is also made necessary by the observation that true *Cancrinella* possesses dorsal spines, as discussed and figured by Grigoryeva et al. (1977, pl. 19, fig 2e).

Western Australian species previously attributed by me to *Cancrinella* lack dorsal spines and appear to fall into three groups as follows.

1. A group of species with fine costellae, low narrow rugae and recumbent ventral spines with distinct spine ridges. Dorsal valves possess costellae and dimples and are very gently geniculate. These forms, which are now attributed to *Costatumulus*, include *Cancrinella irwinensis* Archbold, 1983, *Cancrinella* sp. A of Archbold (1983), and *Costatumulus occidentalis* sp. nov.

2. A rare species, described as *Cancrinella* sp. B by Archbold (1983), with coarse, prominent ventral rugae. This species is referred herein to *Magniplicatina* Waterhouse, 1983b.

Fig. 8. A–E, H, I, K, *Wyndhamia multispinifera* (Prendergast). A, UWA 34457, dorsal valve, interior view, × 1.2. B, C, UWA 34454, ventral valve in ventral and interior views, × 1.3 and × 1.1. D, E, UWA 29057, ventral valve internal mould in ventral and anteroventral views, × 1. H, UWA 34456, dorsal valve, interior view, × 1.1. I, K, UWA 34455, ventral valve in interior and ventral views. × 1.2 and × 1.25. F, G, J, L, *Wyndhamia* sp. A. F, G, J, UWA 27454a, ventral valve in interior, ventral and posteroventral views, × 1.25, × 1 and × 1. L, UWA 27454b, dorsal valve, interior view, × 1.1.

---

3. A group of distinctive species with strongly enrolled ventral valves and with dorsal valves that lack spines, have a flat visceral disc and a striking geniculation anteriorly. These species, herein referred to *Coolkilella* gen. nov., include *Cancrinella coolkilyaensis* Archbold, 1983 and *Productus bellus* Etheridge, 1918.

Whether the above genera should be treated as subgenera is perhaps arguable but in this study they are accepted as being of generic rank.

Costatumulus occidentalis sp. nov.

Fig. 9A–I

Linoproductus lyoni.—Coleman 1957 (*partim*): 76, pl. 8, figs 16–19, 22 (*non* 20, 21).
Lyonia lyoni.—Archbold 1983 (partim): 244.

Holotype. UWA 32025, an internal mould of a complete shell and the external mould of the dorsal valve, from Glendevon Homestead, Woolaga Creek, Irwin River area; High Cliff Sandstone (previously thought to be Fossil Cliff Formation), Aktastinian (Early Artinskian).

Other material. Paratypes: a ventral valve internal mould (UWA 32028) and an incomplete dorsal valve external mould (UWA 32028a).

Measurements (in mm).

Specimen	Hinge width	Maximum width	Ventral height	Dorsal height
UWA 32025	43	48	38	36
UWA 32028	43.5	47	38	—
UWA 32028A	—	—	—	33.5

Description. Large species, transverse in outline, hinge wide, maximum width of shell at mid-length. Relatively gently concavo-convex for genus.

Ventral valve evenly convex from umbo. Transverse profile evenly arcuate, no sulcus. Umbo low, protruding weakly above hinge line. Ears distinct, sharply demarcated from lateral flanks. Distinct row of hinge spines. Interior of valve reflects external ornament, muscle scars not developed.

Costellae prominent over ventral valve, absent on ears, rounded in cross section with narrow intercostal troughs, 10 per 5 mm at 15 mm

from umbo, 8 per 5 mm at anterior of valve. Spine ridges higher and wider than costellae, arising anterior to spine ridges. Spine ridges up to 4.5 mm in length at anterior of ventral valve. Rugae prominent on ears, weaker over venter, relatively fine overall.

Dorsal valve gently concave with weak geniculation at anterior of valve. External ornament of costellae, rugae and dimples mirroring the ventral valve ornament. Ears weakly demarcated from visceral disc. Dorsal interior with median septum approximately half as long as visceral disc. Cardinal process poorly known, appears to be typically linoproductid.

Comments. Costatumulus occidentalis sp. nov. is larger than the other Western Australia species *C. irwinensis* (Archbold) and the poorly known *Cancrinella* sp. A (Archbold 1983). *C. tumulus* (Waterhouse) from the Artinskian Tiverton Formation of the Bowen Basin, Queensland, possesses finer costellae than the new species.

Costatumulus apparently occurs also in northeastern Siberia in the Permian of Verkhoyanya. Some specimens referred to *Cancrinella grandis* Solomina, 1981 (see Abramov & Grigoryeva 1988: 123, pl. 10, fig. 19, pl. 11, figs 1–4) appear to lack dorsal spines and recall *C. occidentalis* in size and ornament, although costellae are finer on the specimens described by Abramov & Grigoryeva. The type specimens of *C. grandis* possess dorsal spines (Solomina 1981).

*Zone. Neochonetes (Sommeriella)* sp. nov. A Zone. Aktastinian (Early Artinskian).

Genus Coolkilella gen. nov.

*Type species. Cancrinella coolkilyaensis* Archbold, 1983.

Diagnosis. Auriculispininae with strongly enrolled ventral valve and dorsal valve with flat or very gently concave visceral disc and pronounced geniculation anteriorly. Ventral spines present but dorsal spines absent. Ventral rugae weakly developed.

Discussion. With the restriction of *Cancrinella* to species with dorsal spines, a distinctive group
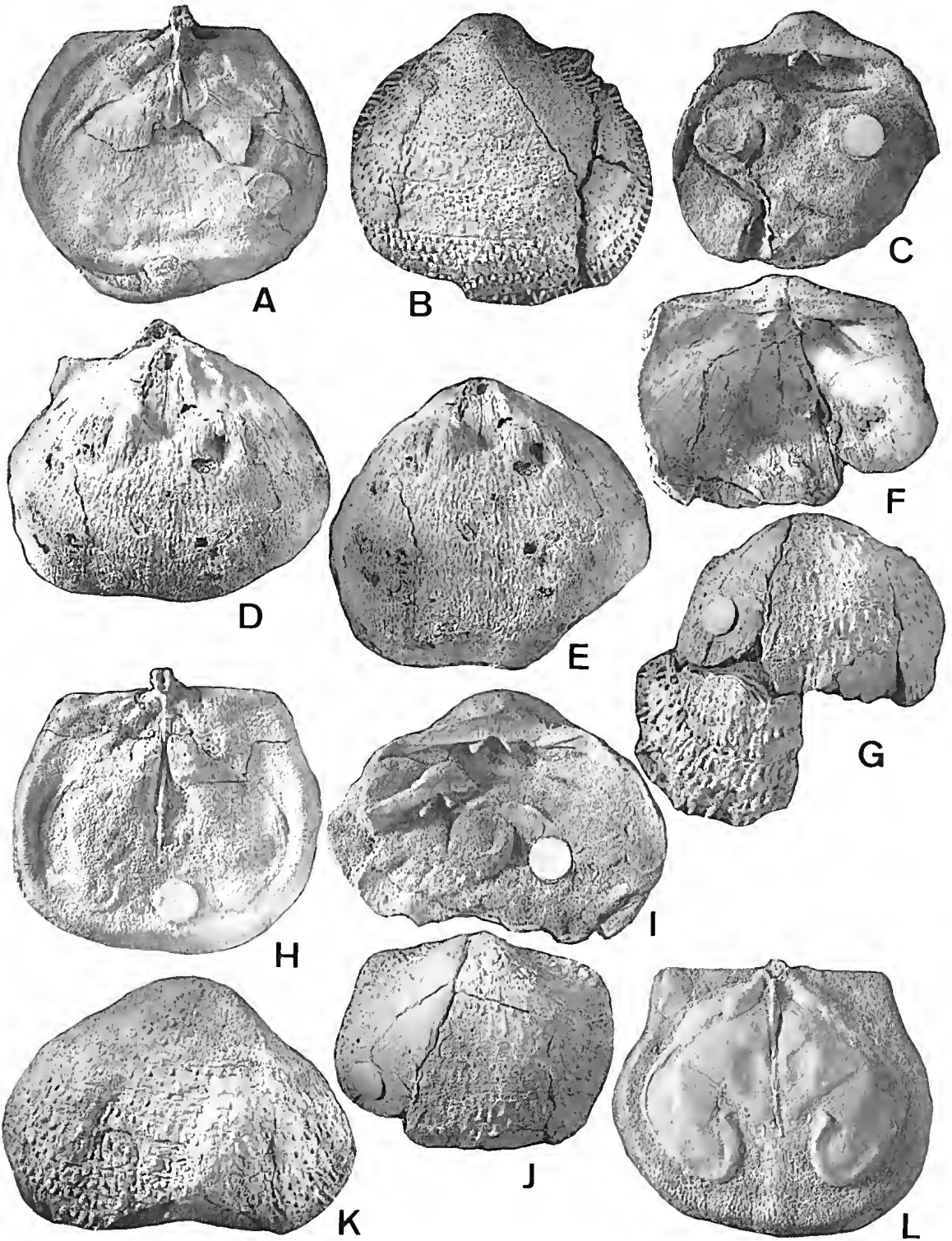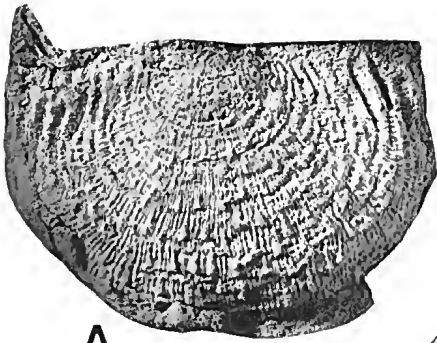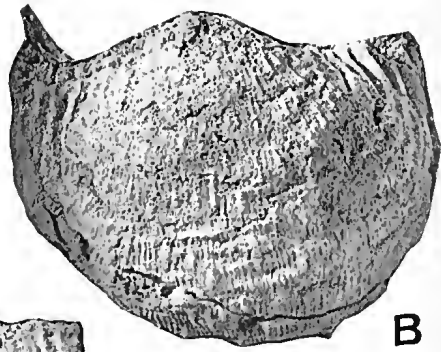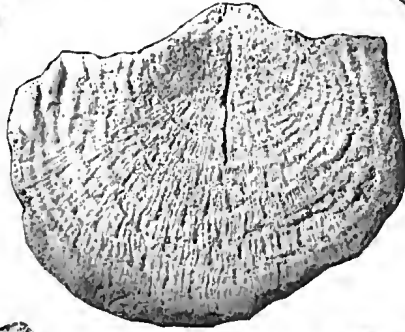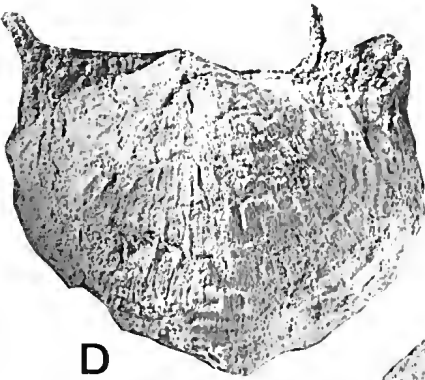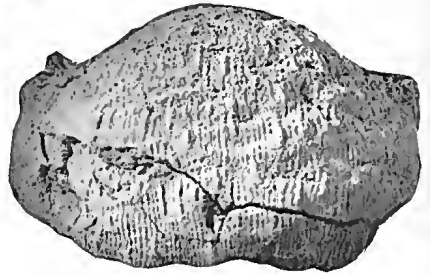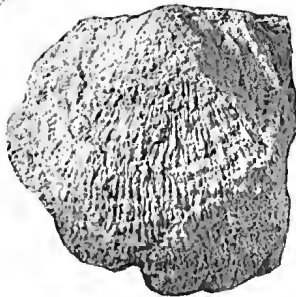
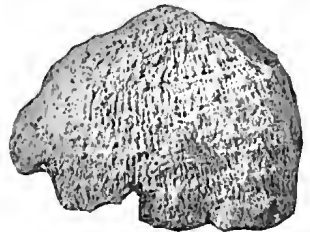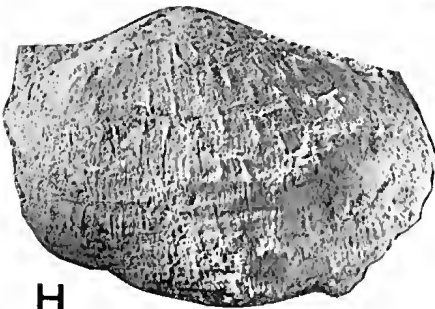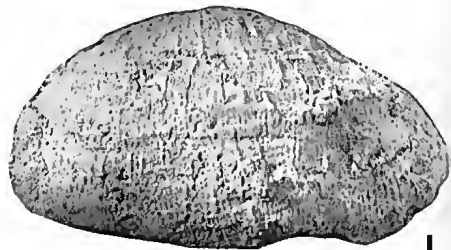*Fig. 9. Costatumulus occidentalis* sp. nov. A–C, E, UWA 32025, holotype, dorsal valve external mould and internal mould of shell in ventral, dorsal and anterior views, × 1.1. D, H, I, UWA 32028, ventral valve internal mould in ventral, anteroventral and anterior views, × 1.1. F, G, UWA 32028a, incomplete dorsal valve external mould in full and anterior views, × 1.1.

of Western Australian species requires a new generic name. Neither *Costatumulus* nor *Magniplicatina* are suitable, as implied above. Ganelin (in Kashik 1990) has proposed the generic names *Kolymaella* and *Omolonia* for certain species previously included in *Cancrinella*. *Kolymaella*, with type species *Cancrinella ogonerensis* Zavodovsky (1960a: 65, pl. 1, figs 13, 14), recalls *Costatumulus* and appears to lack dorsal spines. The dorsal valve is very gently geniculated. *Omolonia*, with type species *Cancrinella snjatkovi* Zavodovsky (1960c: 323 pl. 79, figs 7–9), represents a distinctive form with numerous fine spines with short spine bases closely scattered over the ventral valve and hence is not close to *Coolkilella* gen. nov.

The most striking feature of *Coolkilella coolkilyaensis*, from the Kungurian Coolkilya Formation of the Carnarvon Basin, is the extraordinary development of the geniculation at the anterior of the essentially flat visceral disc (Archbold 1983, fig. 2M–O). This feature of the dorsal valve recalls *Terrakea* Booker, 1930 but that genus possesses prominent dorsal spines, unlike *Coolkilella*.

Coolkilella bella (Etheridge, 1918)

Fig. 10A–C

Cancrinella bella.—Archbold 1983: 241, figs 1Q–X, 2A, B (with synonymy).

Comments. My earlier review of this species was primarily restricted to specimens from the Noonkanbah Formation, Canning Basin (Archbold 1983). Coleman (1957) described specimens of this species from the Wandagee Formation, Carnarvon Basin. One of those specimens is refigured herein in order to illustrate the strongly enrolled nature of the ventral valve and the distinctive ornament of ventral spine bases that normally give rise to one costella at the anterior of each base. The strongly developed dorsal geniculation of the dorsal valve of *Coolkilella bella* was illustrated by Coleman (1957, pl. 8, figs 5, 6) in a submature dorsal valve.

Coolkilella bella is distinguished from *C. coolkilyaensis* by the former species' extremely weakly developed ventral rugae across the venter. *Cancrinella* sp. of Archbold (1982b, pl.

2, figs 12–19) from the Late Artinskian or Early Kungurian of Irian Jaya may be allied to *Coolkilella* as it possesses spine bases that often give rise to only a single costella. The dorsal valve of the Irian Jayan species is unknown.

Zone. Fusispirifer wandageensis Zone. Latest Artinskian to Early Kungurian.

Superfamily PRODUCTACEA Gray, 1840
Family DICTYOCLOSTIDAE Stehli, 1954

Genus Costiferina Muir-Wood & Cooper, 1960

Type species. Productus indicus Waagen, 1884.

Costiferina wadei (Prendergast, 1943)

Fig. 10D–E

Costiferina wadei.—Archbold 1985: 24, fig. 4A–L (with synonymy).

Comments. Previous descriptions of *C. wadei* by Prendergast (1943), Coleman (1957) and Archbold (1985) did not include precise details of the dorsal valve interior because of a lack of well preserved material. A single dorsal valve (CPC 24519) from AGSO locality KNA 17 (described as a measured section of the Noonkanbah Formation, south of Grant Range, Canning Basin, about 13 km (8 miles) bearing 120° from Mount Anderson homestead, approximately 50 m above the base of the section) provides details of the dorsal interior.

The interior of the dorsal valve is strongly geniculated. The median septum arises at the base of the cardinal process and extends across the visceral disc with a blade-like termination. Adductor scars are distinct and dendritic. Brachial ridges are distinct and arise at a low angle. Posterior lateral ridges are prominent and the marginal ridge on the lateral margins of the visceral disc are low. The coarse costae on the exterior of the trail are reflected on the interior. Details of the dorsal interior confirm the assignment of the species to *Costiferina*.

Zone. As discussed briefly in Archbold (in press), the age of *C. wadei* may be as old as the *Echinalosia prideri* Zone (Early Baigendzhinian, Artinskian) but evidence is equivocal.
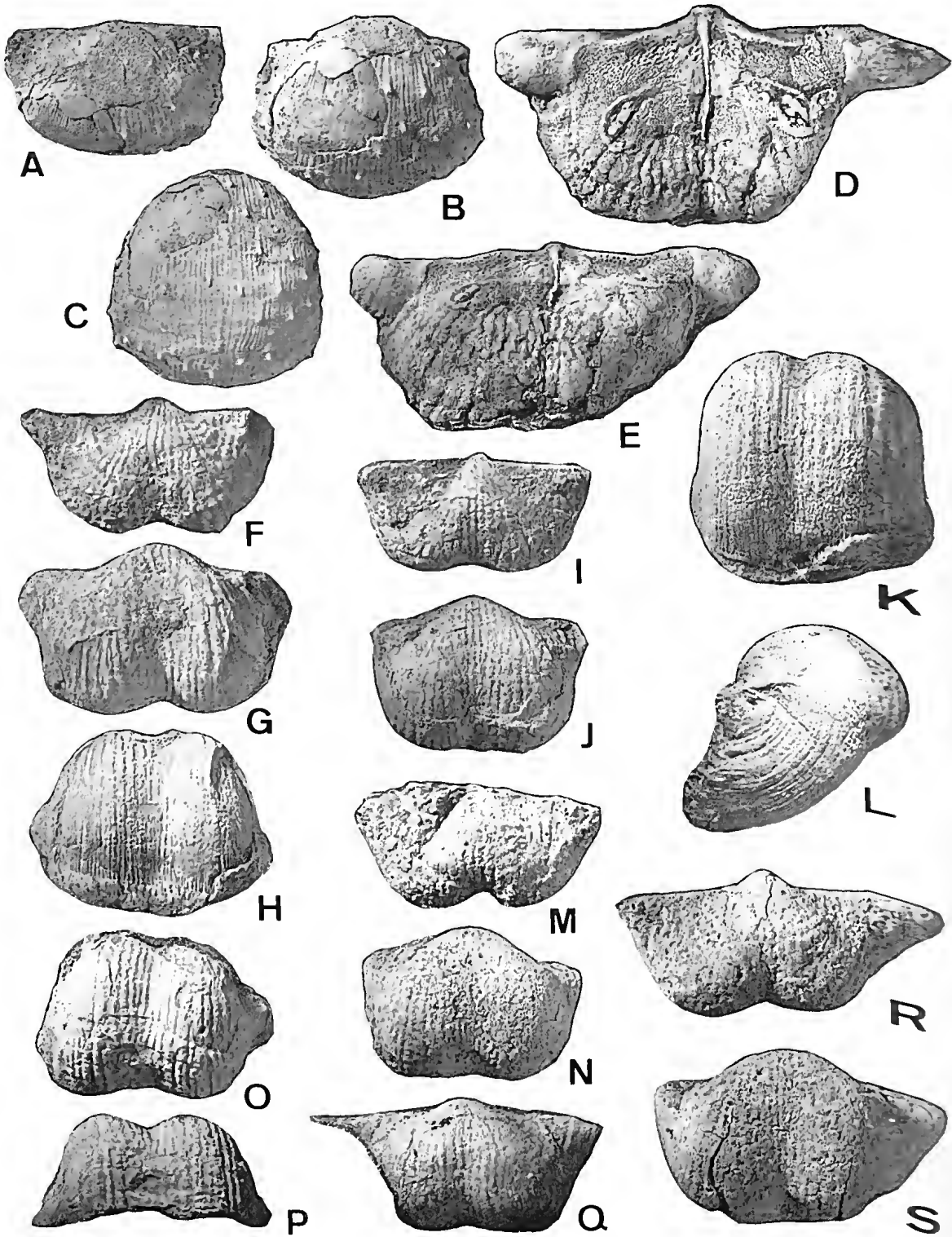
Family MARGINIFERIDAE Stehli, 1954

Genus **Retimarginifera** Waterhouse, 1970

Type species. Retimarginifera perforata Waterhouse, 1970.

Retimarginifera perforata Waterhouse, 1970
Fig. 10F–S

Retimarginifera perforata.—Archbold 1984: 116, fig. 2A–X, AA (with synonymy).

Comments. Two species of *Retimarginifera*, including the type species, are recognised from the Permian of Western Australia (Archbold 1984a). Coleman (1957) and Condon (1967) recorded the genus from various formations in the Carnarvon Basin and Coleman also recorded it from the Noonkanbah Formation of the Canning Basin. My previous review of the genus was only able to confirm the occurrence of the genus in the Cundlego, Wandagee and Coolkilya Formations of the Carnarvon Basin. While searching through the Canning Basin collections of the AGSO, a small suite of specimens was discovered from the Noonkanbah Formation, confirming Coleman's (1957) report. The specimens (CPC 24520–24523, 30868–30870), all from AGSO locality KNA 29 (described as about 13 km bearing 120° from Mount Anderson Homestead, about 277 m (910 feet) above base of measured section), conform to previous descriptions of the species.

Zone. The possibility of recognising zones based on brachiopods within the Noonkanbah Formation was implied by Thomas (1958a: 24), and additional data to support this view are provided by Archbold (in press). The present material probably indicates an horizon in the Noonkanbah Formation belonging to the *Fusispirifer cundlegoensis* Zone.

Family WAAGENOCONCHIDAE Muir-Wood & Cooper, 1960
Subfamily WAAGENOCONCHINAE Muir-Wood & Cooper, 1960

Genus **Waagenoconcha** Chao, 1927

Type species. Productus humboldtii d'Orbigny (1842: 54, pl. 5, figs 4–7) from the early Permian of Yarbichambi, Bolivia.

Comments. The genus has been well described by Coleman (1957), Grant (1966) and Cooper & Grant (1975). The type species has been figured extensively from the type region by Kozlowski (1914, pl. 7, figs 1–9), Muir-Wood & Cooper (1960, pl. 89, figs 6–10), Branisa (1965, pl. 64, figs 11–19) and Samtleben (1971, pl.2, figs 17–19). The syntypic series of d'Orbigny (1842) was refigured by Tschernyschew (1904: 31, figs T1–T3a). No lectotype of *Productus humboldtii* has been selected by subsequent workers, so I select as lectotype the specimen figured by Tschernyschew (1904: 31, figs T1 and T1a). It was said by Tschernyschew to be housed in the d'Orbigny collection of the Museum d'Histoire Naturelle, Paris.

Large Permian specimens from Bear Island figured by Wiman (1914, pl. 14, figs 8, 9, pl. 15, figs 1, 2, pl. 16, figs 1–4) as *P. humboldtii* were named *Ruthenia wimani* by Fredericks (1934: 28). This species was chosen by Waterhouse (1983b: 125) as type species of the new genus *Wimanoconcha*, which was briefly diagnosed as typically possessing an "externally flat, anteriorly thickened dorsal valve, with subcrenulate hinge". An examination of Wiman's excellent illustrations indicates that his specimens are gerontic individuals. Large dendritic adductor scars and distinct brachial ridges are present in the dorsal valve, which is gently concave externally with a distinct median fold. The hinge line is straight and the ventral sulcus is distinct early in ontogeny but flattens out anteriorly in gerontic specimens.

Wimanoconcha appears to have value as a subgenus of *Waagenoconcha*, but for reasons different to those provided by Waterhouse (1983b). Large species of *Waagenoconcha* typically possess a long trail with crenulations developing radially on the flanks and centre of the trail (Wiman 1914, pl. 15, fig. 1, pl. 16, fig. 2). Dorsal valves may develop weak crenulations at

---

Fig. 10. A–C, *Coolkilella bella* (Etheridge), AMF 38455, ventral valve in posterior, ventral and anteroventral views, × 1.25. D, E, *Costiferina wadei* (Prendergast), CPC 24519, dorsal valve in interior and anterior views, × 1. F–S, *Retimarginifera perforata* Waterhouse. F–H, CPC 24520, ventral valve in posterior, ventral and anterior view, × 2. I, J, CPC 24521, ventral valve in posterior and ventral views, × 2. K, L, CPC 24522, ventral valve in anterior and lateral views, × 2. M, N, CPC 24523, ventral valve in posterior and ventral views, × 2. O, P, CPC 30868, ventral valve in ventral and anterior views, × 2. Q, CPC 30869, ventral valve in ventral view, × 2. R, S, CPC 30870, ventral valve in posterior and ventral views, × 2.

the anterior margin (Kalashnikov 1986, pl. 121, fig. 7b) and become thickened anteriorly and internally in the region of the visceral disc. These distinctions serve to characterise the subgenus *Wimanoconcha*.

Subgenus Waagenoconcha (Wimanoconcha) Waterhouse, 1983

Type species. Ruthenia wimani Fredericks, 1934.

Comments. Large specimens referred to Fredericks's species have been recorded throughout the Arctic from areas such as East Greenland (Dunbar 1955), Spitzbergen (Stepanov 1936, Gobbett 1964), the northern Timan (Kalashnikov 1986), the Pechora Basin and the Pay-Khoy (Ifanova 1972, Solomina 1960), the Taimyr Peninsula (Einor 1946), the Verkhoyansk (Abramov & Grigoryeva 1988) and the Kolyma–Omolon region (Sarycheva 1984). Large species from Inner Mongolia attributed to *Waagenoconcha* (Lee et al. 1984, 1985) also belong in *Wimanoconcha*. Specimens referred to various varieties of *Productus (Ruthenia) purdoni* by Reed (1944, pl. 13, figs 1–6, pl. 14, figs 1–6) from the Salt Range, Pakistan, are also allied.

Based on the new material illustrated herein, the Western Australian species *Waagenoconcha imperfecta* Prendergast is assigned to *Wimanoconcha* on the basis of the morphology of mature specimens.

Waagenoconcha (Wimanoconcha) imperfecta Prendergast, 1935

Figs 11A–H, 12A–K, 13A–G

Waagenoconcha imperfecta Prendergast 1935: 15, pl. 4, figs 1–3.—Prendergast 1943: 25, pl. 3, figs 7–9.—Coleman 1957: 82, pl. 10, figs 8–14, pl. 11, figs 1–6.—Archbold 1988: 22.
Waagenoconcha vagans.—Prendergast 1943: 26, pl. 3, fig. 6.
cf. *Waagenoconcha imperfecta.*—Tazawa 1974: 127, pl. 1, figs 4–6, pl. 2, figs 2–7, pl. 3, figs 1–3, pl. 4, figs 1–4, 7.

Holotype. A submature shell, UWA 3044, from Luluigui Station, west Kimberley district; Hardman Formation, Cherrabun Member, Canning Basin.

Material. CPC 30871–30872, two internal moulds of shells from AGSO Locality KLC 42, near Tutu Bore, Nerrima Station, on flank of Dry Corner Syncline, north-west of Nerrima Dome. CPC 30873, an internal mould of a dorsal valve from AGSO locality M3, Lat. 19°12′S, Long. 125°32′E, central Millyit Range. CPC 30874–30884, a ventral valve, five complete dorsal valves, four incomplete dorsal valves and an external mould of a dorsal valve, all from AGSO locality KLB 11, from beds 1.25 m thick at about 40 m below top of Mount Hardman. All Cherrabun Member of Hardman Formation, Canning Basin.

CPC 30885–30886, a dorsal valve internal mould and an incomplete ventral valve internal mould, from AGSO locality PK1, Tchindi Beach, west of Port Keats Mission. CPC 30887–30888, two fragments of dorsal valves, from AGSO locality PK4 on coast approximately 13.5 km north of Cape Dombey, Port Keats area, Northern Territory. Upper Marine Beds, Port Keats Group.

Comments. This species was described by previous authors (Prendergast 1935, 1943; Coleman 1957) on the basis of chiefly submature individuals. The new material illustrated herein provides additional details on the maximum size of individuals and the nature of mature dorsal valves, and documents the species from the Port Keats Group.

The largest of the specimens show the development of radial crenulations of the shell on the flanks of the ventral trail (Fig. 11A, H). The ventral sulcus also flattens anteriorly on these specimens. Mature dorsal valves show the initial appearance of visible brachial ridges (Figs 11A, 13A, C). The cardinal process develops from a short, weakly lobate structure in juvenile specimens (Figs 12C, 13E) to a strongly trilobate feature at submaturity (Fig. 12D–H). Gerontic dorsal valves show distinct thickening of the valve and the cardinal process takes on a blunt appearance (Fig. 13A).

Specimens attributed to *Productus waageni* by Broili (1916, pl. 118, figs 1–5) from the Upper Permian of Timor were considered by Prendergast (1943) and Coleman (1957) to be representatives of *Waagenoconcha (Wimanoconcha) imperfecta*. While the two species are similar in many details, they are distinguished by the nature of the spine bases (see Archbold & Bird 1989).

Tazawa (1974) referred to *Waagenoconcha (Wimanoconcha) imperfecta* an extensive suite of specimens from the upper part of the Lower Kanokura Series, southern Kitakami Mountains, north-east Japan. The specimens are gen-

Fig. 11. A–H, *Waagenoconcha (Wimanoconcha) imperfecta* Prendergast. A–D, CPC 30871, internal mould of shell in dorsal, ventral, profile and posterior views, × 1. E, CPC 30872, internal mould of shell in ventral view, × 1.2. F–H, CPC 30873, ventral valve in posterior, ventral and profile views, × 1.
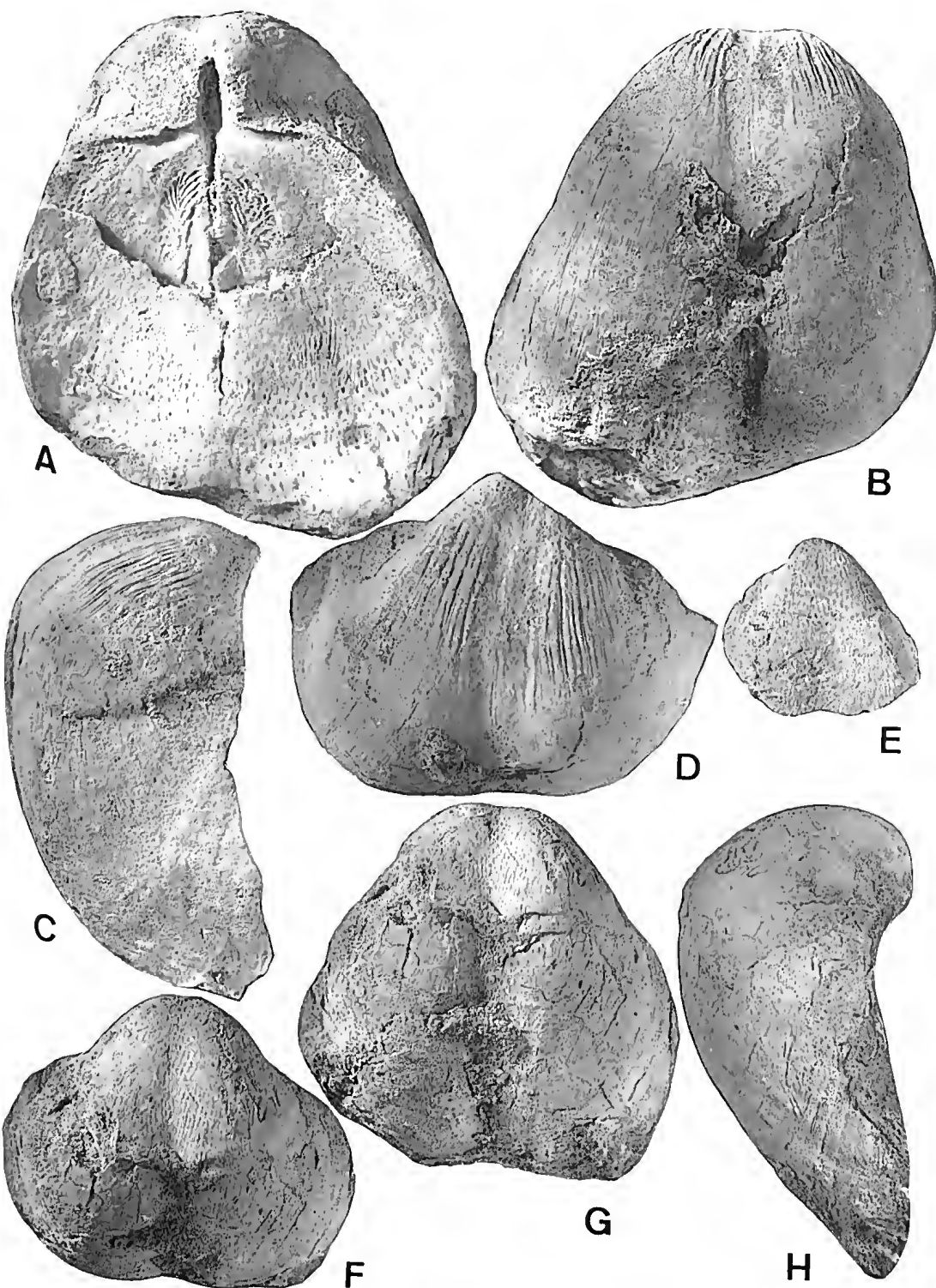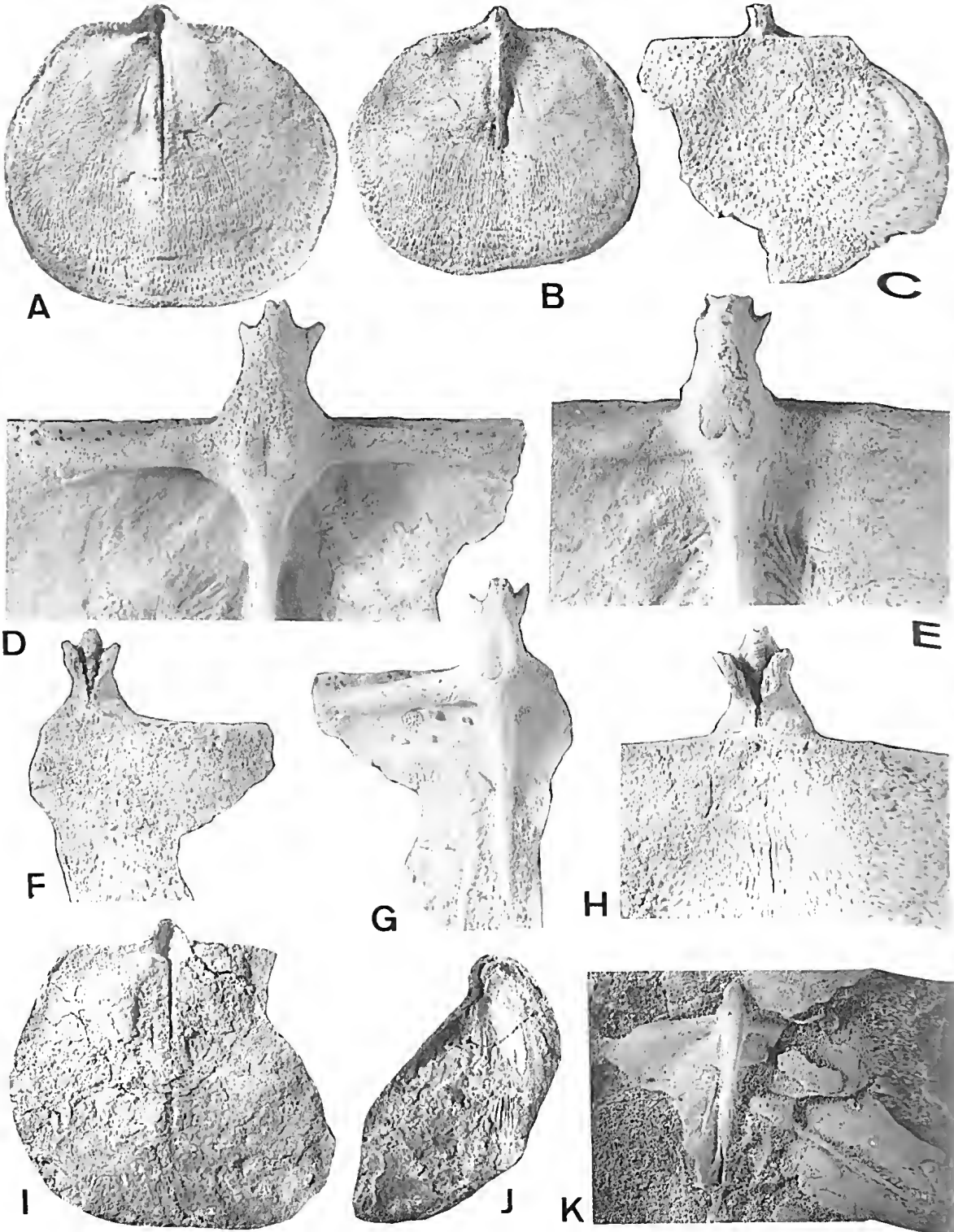
Fig. 12. A–K, *Waagenoconcha (Wimanoconcha) imperfecta* Prendergast. A, B, CPC 30874, internal mould of dorsal valve and latex cast from mould, × 1.3 and × 1.1. C, CPC 30880, juvenile dorsal valve in dorsal view, × 3.2. D, H, CPC 30881, cardinal process of incomplete dorsal valve, × 3.5. E, CPC 30882, cardinal process of incomplete dorsal valve, × 3.5. F, G, CPC 30883, cardinal process of incomplete dorsal valve, × 3.2. I, CPC 30885, internal mould of dorsal valve, × 1. J, CPC 30886, incomplete internal mould of ventral valve, × 1. K, CPC 30887 and CPC 30888, incomplete fragments of dorsal valves, × 1.

---

erally smaller than Australian material but otherwise are close. I leave them as a comparison in the synonymy above.

Waterhouse (1969a: 723; 1982a: 41, pl. 8, fig. a) attributed a poorly preserved, incomplete ventral valve and numerous "fragments of external moulds" from the Arthurton Group, New Zealand, to *Waagenoconcha* aff. *imperfecta*. Examination of a latex cast of the figured ventral valve (supplied by Dr Hamish Campbell, New Zealand Geological Survey) indicates that the specimen may be a waagenoconchinid but that the generic and specific identifications are premature and should await the discovery of additional well preserved specimens.

Zone. Waagenoconcha (Wimanoconcha) imperfecta Zone (Archbold 1988a). This zone, of Djhulfian age, is the youngest marine Permian zone of the Australian continent (Archbold in press).

Order SPIRIFERIDA Waagen, 1883
Suborder SPIRIFERIDINA Waagen, 1883
Superfamily SYRINGOTHYRIDACEA Fredericks, 1926
Family SYRINGOTHYRIDIDAE Fredericks, 1926
Subfamily PERMOSYRINXINAE Waterhouse, 1986

Genus **Cyrtella** Fredericks, 1924

Type species. Cyrtia kulikiana Fredericks, 1916.

Cyrtella sp.

Fig. 14A–C

Comments. Two specimens (NMV P120351, a dorsal valve, and GSWA 43869, a broken ventral valve) from the Fossil Cliff Formation, Perth Basin, are figured in order to document the occurrence of *Cyrtella*, or a related genus, from the formation. The two specimens are inadequate for detailed comparison with the Carnarvon Basin Tastubian–Sterlitamakian species *Cyrtella australis* Thomas, 1971 or the Sterlitamakian Canning Basin species *Cyrtella koopi* Archbold, 1990, but the costal details suggest a closer relationship with the former species.

Zone. Strophalosia irwinensis Zone. Sterlitamakian.

Superfamily SPIRIFERACEA King, 1846
Family SPIRIFERIDAE King, 1846
Subfamily SPIRIFERELLINAE Waterhouse, 1968

Genus **Spiriferella** Tschernyschew, 1902

Type species. Spirifer saranae de Verneuil, in Murchison et al. 1845.

Spiriferella australasica (Etheridge, 1889)

Fig. 14D–G

Spiriferella australasica.—Archbold & Thomas 1985a: 39, figs 1BB–HH, 2A–M (with synonymy).

Comments. A single specimen (WAM 87.475) from the Wandagee Formation at a general locality on the Minilya River, Wandagee Station, Carnarvon Basin is illustrated fully to show the details of the fastigium of the dorsal valve. The fastigium was one of the few details of *S. australasica* not able to be fully described by Archbold & Thomas (1985a). The present specimen shows that a shallow median groove arises on the peak of the fastigium and persists to the anterior margin of the valve, with the anterior margin fold being distinct but flat-topped. Other details of the specimen conform with the species description provided by Archbold & Thomas (1985a).

Zone. Fusispirifer wandageensis Zone. Latest Baigendzhinian to earliest Kungurian.

Subfamily NEOSPIRIFERINAE Waterhouse, 1968

Genus **Cartorhium** Cooper & Grant, 1976

Type species. Cartorhium retusum Cooper & Grant, 1976.

Comments. The genus was fully described by Cooper & Grant (1976). The new species described below is based on a single remarkable specimen that does not readily fall into any other genus of the Neospiriferinae, as defined by
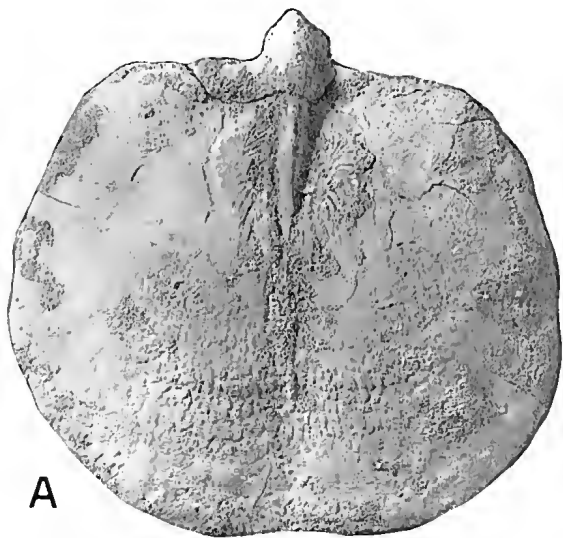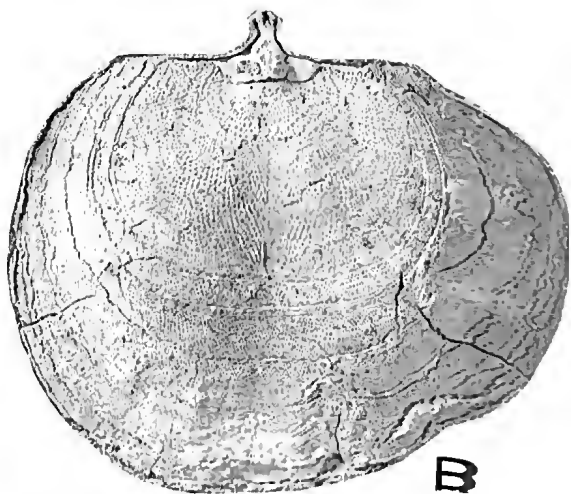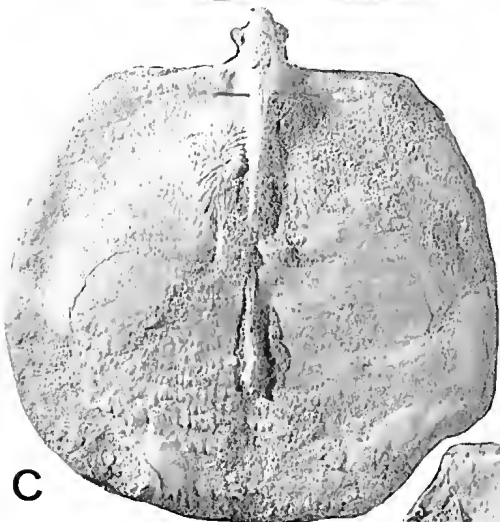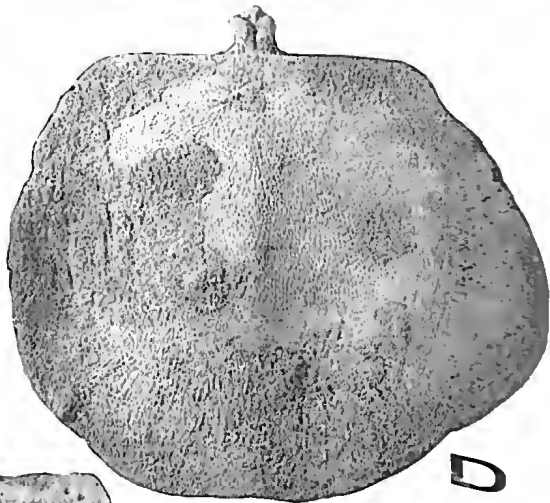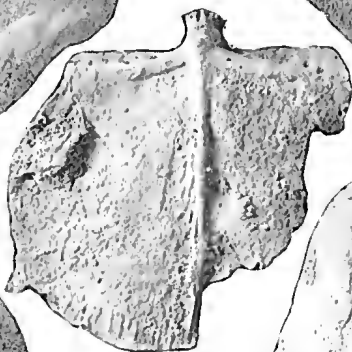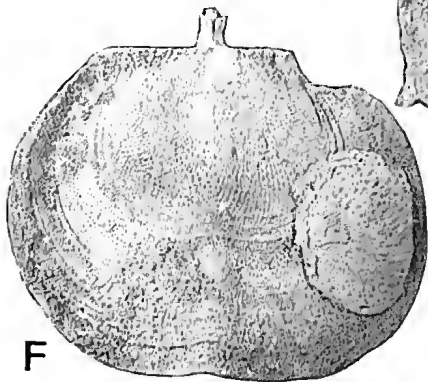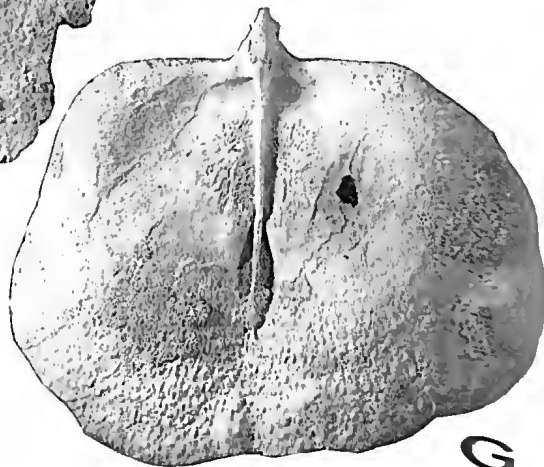
Archbold & Thomas (1984b). Although only one specimen is available, it is so unlike any other Western Australian neospiriferid that it is formally named as a new species.

Cartorhium imperfectum sp. nov.

Fig. 14H–K

Holotype. NMV P120352, an internal mould of a conjoined shell with portion of the shell remaining near the umbonal regions, from UWA locality WC 19, north-east of east fence of Mungadan Paddock, Wandagee Station; Wandagee Formation, Carnarvon Basin. Collector Dr C. Teichert.

Measurements. Maximum width, 53.0 mm estimate; hinge width, 40 mm estimate; height of ventral valve, 37.8 mm; height of dorsal valve, 35.2 mm; thickness of shell, 24.9 mm.

Description. Moderate sized species, transversely subelliptical. Maximum width at approximately half shell length. Hinge width relatively narrow. Ears absent.

Ventral umbo small, rounded and overhanging low, relatively narrow interarea. Sulcus absent at early ontogenetic stages, anteriorly developed as a broad flattening of valve with a broad weakly developed sulcal tongue. Ventral valve flanks barely plicate. Costae equidimensional, bifurcate once early in ontogeny and once more later in ontogeny, resulting in fascicles of normally 4 costae at anterior margin of valve. Costae broad, rounded with narrow intercostal troughs, between 6 and 7 costae per cm at anterior of valve. Ventral interior apical structures unknown.

Dorsal fastigium barely discernible from lateral flanks of dorsal valve, resulting in low, broad fold at anterior margin. Lateral plications not developed on valve flanks. Costae on anterior of valve comparable to ventral costae. Dorsal apical structures not known except for delicate median myophragm extending for 12 mm anterior to cardinal process.

Discussion. The specimen appears most closely allied to species of *Cartorhium* but differs in its finer costae and broader anterior sulcus and low, broad fold. Species assigned by Reed (1944) to *Purdonella* are also allied but again do not possess a low, broad fold.

Zone. Fusispirifer wandageensis Zone. Latest Baigendzhinian to Early Kungurian.

Superfamily uncertain
Family INGELARELLIDAE Campbell, 1959
Subfamily INGELARELLINAE Campbell, 1959

Genus Tomiopsis Benediktova, 1956

Type species. Brachythyris kumpani Yanishevskiy. 1935.

Tomiopsis hardmani Archbold & Thomas, 1986

Fig. 14L, M

Comments. This species was fully described by Archbold & Thomas (1986a) but the micro-ornament was poorly known. A single natural cast of a dorsal valve (CPC 19851) from AGSO locality CR 1565, described as Lat. 19°04′00″S, Long. 125°08′30″E, Kirkby Range Member, Hardman Formation, Canning Basin, Crossland mapsheet area, provides details of the micro-ornament. This consists of elongate, narrow, shallow surface grooves arranged in a subquincunx pattern and hence is diagnostic of *Tomiopsis*.

Zone. The species occurs in both the *Liveringia magnifica* and *Waagenoconcha (Wimanoconcha) imperfecta* Zones of Archbold (1988a). Midian to Djhulfian.

Superfamily RETICULARIACEA Waagen, 1883
Family ELYTHIDAE Fredericks, 1924
Subfamily ELYTHINAE Fredericks, 1924

Genus Spirelytha Fredericks, 1924

Type species. Spirelytha pavlovae Archbold & Thomas, 1984.

Spirelytha kashirtsevi sp. nov.

Fig. 15A–D

Spirelytha sp. B.—Archbold & Thomas 1984a: 322, fig. 4X–Z, AA.

Holotype. A natural cast of a shell, CPC 24231, from the Quinnanie Shale, Carnarvon Basin. Full locality

Fig. 13. A–G, *Waagenoconcha (Wimanoconcha) imperfecta* Prendergast. A, CPC 30875, gerontic dorsal valve, interior view, × 1. B, CPC 30884, external mould of large dorsal valve, × 1. C, CPC 30876, dorsal valve, interior view, × 1. D, CPC 30877, dorsal valve external view, × 1. E, CPC 30880, juvenile dorsal valve, interior view, × 3.2. F, CPC 30878, submature dorsal valve, exterior view, × 1. G, CPC 30879, mature dorsal valve, interior view, × 1.
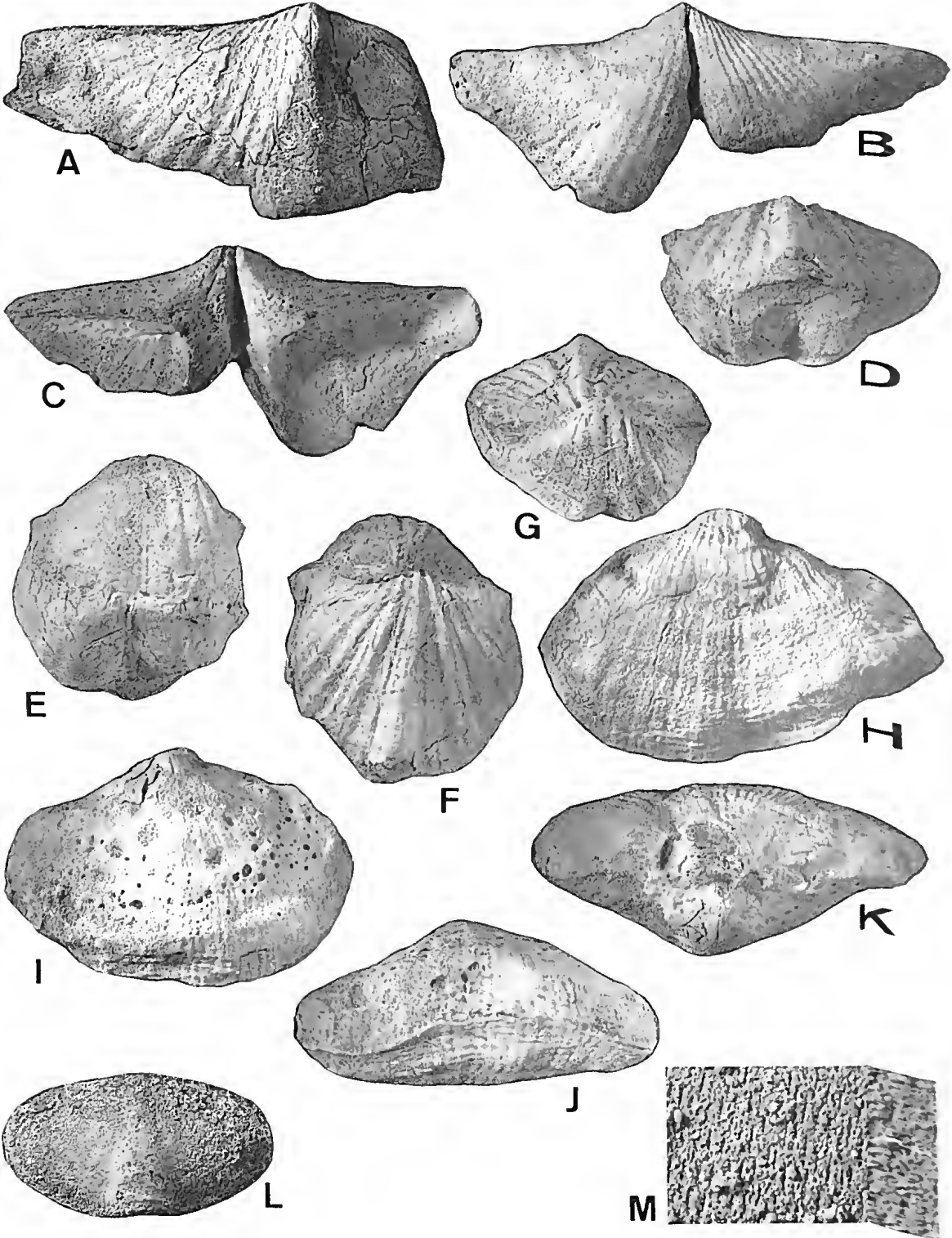
Fig. 14. A–C, *Cyrtella* sp. A, NMV P120351, incomplete dorsal valve in dorsal view, × 1. B, C, GSWA 43869, broken ventral valve in ventral and dorsal views, × 1.3. D–G, *Spiriferella australasica* (Etheridge), WAM 87.475, shell in ventral, dorsal, posterior and anterior views, × 1. H–K, *Cartorhium imperfectum* sp. nov., NMV P120352, holotype, internal mould of shell in ventral, dorsal, anterior and posterior views, × 1. L, M, *Tomiopsis hardmani* Archbold & Thomas, natural east of dorsal valve, × 1, and portion of surface enlarged, × 8.

---

details were provided by Archbold & Thomas (1984a).

Etymology. For Arkady Sergeevich Kashirtsev, Soviet palaeontologist and geologist.

Measurements. Maximum width, 23.5 mm; hinge width, 15.5 mm; height of ventral valve, 17.5 mm; height of dorsal valve, 17.4 mm; thickness, 12.0 mm.

Diagnosis. Equally convex valves with ventral interarea at 90° to plane of dorsal valve. Moderate size for genus, transversely oval in outline. Ventral umbo low, pointed and overhanging interarea. Sulcus distinct, broad, U-shaped in cross section. Delthyrium large, triangular. Dorsal umbo small, sharp. Fastigium very low, only visible on anterior half of valve. Fold low, rounded.

Concentric lamellae coarse, about 7 per cm at 1.5 cm from umbones, carrying poorly preserved biramous spine bases, about 2 per mm at 1 cm from umbones. Interior unknown. Anterior commissure parasulcate.

Discussion. Archbold & Thomas (1984a) noted that this specimen represented a separate species, which is now named because of its distinct biconvex profile, comparable size of both valves and consequent angle of the ventral interarea to the plane of the dorsal valve.

Most literature on *Spirelytha* was reviewed by Archbold & Thomas (1984a) but it is noted herein that Kashirtsev (1955) recorded the genus from north-eastern Russia. Since the 1984 review, two Western Australian species have been recorded from north-eastern Russia, namely *Spirelytha fredericksi* by Klets (1987) and *S. miloradovichi* by Abramov & Grigoryeva (1988).

Zone. Fusispirifer cundlegoensis Zone. Late Baigendzhinian.

Fig. 15. A–D, *Spirelytha kashirtsevi* sp. nov., CPC 24231, holotype, natural east of shell in dorsal, profile, posterior and ventral view, × 2.

ACKNOWLEDGEMENTS

REFERENCES

References are supplementary to those in Parts 1–10 (*Proceedings of the Royal Society of Victoria*, vol. 91: 181; vol. 93: 109; vol. 95: 237; vol.

96: 83; vol. 97: 19; vol. 98: 97; vol. 99: 19; vol. 100: 21; vol. 102: 1; vol. 103: 55).

AFANASYEVA, G. A., 1988. Brakhiopody otryada Chonetida. *Trudy paleontologicheskogo instituta, Akademiya nauk SSSR* 228: 1–123.

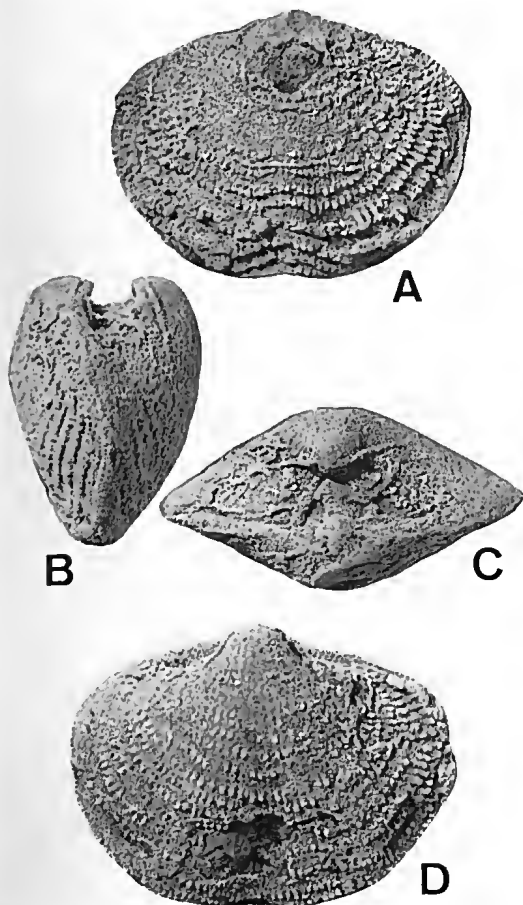ARCHBOLD, N. W., 1981d. Studies on Western Australian Permian brachiopods 2. The family Rugososchonetidae Muir-Wood 1962. *Proceedings of the Royal Society of Victoria* 93: 109–128.

ARCHBOLD, N. W., 1984a. Western Australian occurrences of the Permian brachiopod genus *Retimarginifera*. *Alcheringa* 8: 113–122.

ARCHBOLD, N. W., 1988a. Studies on Western Australian Permian brachiopods 8. The Late Permian brachiopod fauna of the Kirkby Range Member, Canning Basin. *Proceedings of the Royal Society of Victoria* 100: 21–32.

ARCHBOLD, N. W., 1990. Studies on Western Australian Permian brachiopods 9. The Sterlitamakian brachiopod fauna of the Cuneudgerie Sandstone, Canning Basin. *Proceedings of the Royal Society of Victoria* 102: 1–13.

ARCHBOLD, N. W., in press. A zonation of the Permian brachiopod faunas of Western Australia. In *Gondwana 8: Assembly, Evolution and Dispersal*, R. H. Findley, M. R. Banks, J. J. Veevers & R. Unrug, eds, A. A. Balkema, Rotterdam.

ARCHBOLD, N. W. & BIRD, P. R., 1989. Permian Brachiopoda from near Kasliu Village, West Timor. *Alcheringa* 13: 103–123.

ARCHBOLD, N. W. & THOMAS, G. A., 1985a. Permian Spiriferellinae (Brachiopoda) from Western Australia. *Alcheringa* 9: 35–48.

ARCHBOLD, N. W. & THOMAS, G. A., 1986a. Permian Ingelarellidae (Brachiopoda) from Western Australia and Argentina. *Journal of Paleontology* 60: 581–605.

BENEDIKTOVA, R. N., 1956. Spiriferidy Ostrogskoi svity Kuzbassa. In *Materialy vtorogo soveshcheniya po stratigrafii uglenosnykh otlozhenii (Voprosy geologii Kuzbassa* 1), Ugletekhizdat, Moscow, 169–182.

BRANISA, L., 1965. Los fosiles guias de Bolivia. 1. Paleozoico. *Servicio Geologico de Bolivia, Boletin* 6: 1–250.

CAMPBELL, K. S. W., 1959. The *Martiniopsis*-like spiriferids of the Queensland Permian. *Palaeontology* 1: 333–350.

COOPER, G. A. & GRANT, R. E., 1976. Permian brachiopods of West Texas, 4. *Smithsonian Contributions to Paleobiology* 21: 1923–2607.

DING Y.-J., XIA G.-Y., DUAN C.-H., LI W.-G., LIU X.-L. & LIANG Z.-F., 1985. Study on the Early Permian stratigraphy and fauna in Zhesi district, Nei Mongol Zizhiqu (Inner Mongolia). *Bulletin of the Tianjin Institute of Geology and Mineral Resources* 10: 1–241.

EINOR, O. L., 1946. Brakhiopody nizhnego karbona i nizhnei permi zapadnogo Taimyra. *Trudy gorno-geologischeskogo upravleniya* 26: 1–93.

ETHERIDGE, R., Jnr, 1889. Remarks on fossils of Permo-Carboniferous age, from north-western Australia, in the Macleay Museum. *Proceedings of the Linnean Society of New South Wales* 4 (2): 198–214.

FREDERICKS, G. N., 1934. Fauna permskikh otlozhenii Poluostrova Kanina. *Trudy arkticheskogo instituta* 13: 5–42.

GRANT, R. E., 1966. Spine arrangement and life habits of the productoid brachiopod *Waagenoconcha. Journal of Paleontology* 40: 1063–1069.

GRUNT, T. A., SARYCHEVA, T. G. & SOKOLSKAYA, A. N., 1974. Permskaya sistema. Brakhiopody. In *Atlas iskopaemoi fauny Armyanskoi SSR*, V. T. Akopyana, ed., Akademiya nauk Armyanskoi SSR, Yerevan, 127–148.

KALASHNIKOV, N. V., 1986. Brakhiopody. In *Atlas kharakternykh kompleksov permskoi fauny i flory Urala i Russkoi platformy. Trudy vsesoyuznyi ordena Lenina nauchno-issledovatel'skii geologicheskii Institut im. A. P. Karpinskogo* 331: 29–30, 90–94, 231–250.

KASHIK, D. S., 1990. Opornyi razrez permi Omolonskogo Massiva. *Trudy mezhvedomstvennyi stratigraficheskii komitet SSSR* 21: 1–198.

KASHIRTSEV, A. S., 1955. Materialy po stratigrafii i paleontologii verkhnepaleozoiskikh otlozhenii yugo-zapadnogo Verkhoyanya (verkhov'ya basseina r. Tumary). *Trudy Yakutskogo filiala akademiya nauk SSSR* 2: 63–87.

LEE L., GU F. & LI W.-G., 1984. Early Permian productids from Xi Ujimqin Qi, Nei Monggol Autonomous. *Professional Papers of Stratigraphy and Palaeontology* 11: 71–82.

LIKHAREV, B. K., 1931. Materialy k poznaniyu fauny verkhne-permskikh otlozhenii severnogo Kraya. *Trudy glavnogo geologo-razvedochnogo upravleniya VSN Kh. SSSR 71: 1–42.*

RUZHENTSEV, V. E. & SARYCHEVA, T. G., 1965. Razvitie i smena morskikh organizmov na rubeshe paleozoya i mezozoya. *Trudy paleontologicheskogo instituta, Akademiya nauk SSSR* 108: 1–431.

SAMTLEBEN, C., 1971. Zur Kenntnis der Produktiden und Spiriferiden des bolivianischen Unterperms. *Beihefte zum Geologischen Jahrbuch* 111: 1–163.

SARYCHEVA, T. G., 1984. Produktidy roda *Waagenoconcha* Chao v karbone i permi Sibiri i Arktiki. *Trudy paleontologicheskogo instituta, Akademiya nauk SSSR* 199: 120–135.

SOLOMINA, R. V., 1960. Nekotorye permskie brakhiopody Pai-khoya. *Sbornik statei po paleontologii i biostratigrafii* 19: 25–73.

STEPANOV, D. L., 1936. Materialy k poznaniyu brakhiopodovoi fauny verkhnego paleozoya Shpitzbergena. *Uchenye zapiski Leningradskii gosudarstvennyi universitet, Seriya geologo-pochvenno-geograficheskaya* 2: 114–128.

STEPANOV, D. L., KULIKOV, M. V. & SULTANAEV, A. A., 1975. Stratigrafiya i brakhiopody verkhnepermskikh otlozhenii Poluostrova Kanin. *Vest*

nik Leningradskogo universiteta 6: 51–65.

TAZAWA, J.-I., 1974. *Waagenoconcha* (Brachiopoda) from the Permian of the southern Kitakami Mountains, northeast Japan. *Journal of the Faculty of Science Hokkaido University, Series IV, Geology and Mineralogy* 16: 121–143.

TSCHERNYSCHEW, T. N., 1904. Brachiopoda. *Productus humboldtii* d'Orbigny, 1842. *Palaeontologia Universalis.* Centuria 1: 31–31a.

WATERHOUSE, J. E., 1968. The classification and descriptions of Permian Spiriferida (Brachiopoda) from New Zealand. *Palaeontographica Abteilung A* 129: 1–94.

WATERHOUSE, J. B. 1969a. World correlations of New Zealand Permian stages. *New Zealand Journal of Geology and Geophysics* 12: 713–737.

WATERHOUSE, J. B., 1983a. New Permian invertebrate genera from the east Australian segment of Gondwana. *Bulletin of the Indian Geologists' Association* 16: 153–158.

WATERHOUSE, J. B., 1983b. Permian brachiopods from Pija Member, Senja Formation, in Manang district of Nepal, with new brachiopod genera and species from other regions. *Bulletin of the Indian Geologists' Association* 16: 111–151.

WIMAN, C., 1914. Über die Karbonbrachiopoden Spitzbergens und Beeren Eilands. *Nova Acta Regiae Societatis Scientiarum Upsaliensis, Seriei Quartae* 3: 1–91.

YANISHEVSKIY, M. E., 1935. Opisanie fauny iz osnovaniya uglenosnoi tolshi Kuznetskogo Basseina. *Uchenye zapiski Leningradskogo gosudarstvennogo universiteta, Seriya geologo-pochvennykh-geograficheskaya* 1: 53–76.

ZAVODOVSKIY, V. M., 1960e. Novye vidy permskikh linoproduktid Severo-Vostoka SSSR. In *Novye vidy drevnikh rastenii i bespozvonochnykh SSSR, Chast' I,* B. P. Markovskii, ed., Gosudarstvennoe nauchno-tekhnicheskoe izdatel'stvo, Moscow, 320–328, 578–585.

THE TADPOLE OF *LITORIA PHYLLOCHROA* (ANURA: HYLIDAE)

JEAN-MARC HERO[1] AND GRAEME GILLESPIE[2]

[1]Department of Zoology, James Cook University, Townsville, Queensland 4811
[2]Department of Conservation and Natural Resources, 52 Stanley Street, Orbost, Victoria 3888

The tadpole of *Litoria phyllochroa* is described and illustrated from East Gippsland, Victoria. Breeding site characteristics are given for a variety of habitat types. Characteristics distinguishing tadpoles of this species from tadpoles of sympatric *Litoria* species are presented.

LITORIA PHYLLOCHROA (Gunther, 1863) is a small (27–41 mm long; Tyler 1992) green hylid frog found along the coast and hinterland of southern Queensland, New South Wales and eastern Victoria (Brook 1983, Tyler 1992). There is long-standing recognition that two species are presently included under the name *L. phyllochroa*; this paper deals with *L. phyllochroa* Form A of Littlejohn (1967). In Victoria its distribution is generally east and south of the Great Dividing Range (Hero et al. 1991), although some populations occur as far north as the Mitta Mitta area (Atlas of Victorian Wildlife Database, Department of Conservation and Environment Victoria).

Litoria phyllochroa is a member of the *Litoria citropa* species group of Tyler & Davies (1978, 1985), which also comprises *L. subglandulosa, L. pearsoniana* and *L. piperata*. *L. phyllochroa* is morphologically most similar to *L. pearsoniana* from which it can be distinguished by the presence of a green tympanum rather than a brown one (McDonald & Davies 1990). *L. citropa* and *L. phyllochroa* are the only members of this species group currently recognised as occurring in Victoria. A possible addition to this species group is *Litoria spenceri*, which was suggested by Copland (1957) to be related to *L. citropa*. These two species have very similar biphasic advertisement calls (Watson et al. 1991) and similar life histories (personal observation). The tadpole of *L. spenceri* is also morphologically very similar to that of *L. phyllochroa* (Hero et al. in prep.)

Litoria phyllochroa, L. piperata and *L. spenceri* are the only species of this group for which the tadpoles have not been described. We present a diagnosis and description of the tadpole of *L. phyllochroa* from Victoria, indicating features which distinguish it from sympatric lotic hylid species and from other species in the *L. citropa*

group, and the habitats where it was found in eastern Victoria.

METHODS

Tadpoles were collected in the summers of 1989/1990, 1990/1991 and 1991/1992 at several locations in Central and East Gippsland (Fig. 1, Table 1). At each collection site the location of tadpoles in the stream, the micro-habitat, the presence of other tadpole species and the presence of fish were noted. A brief description of
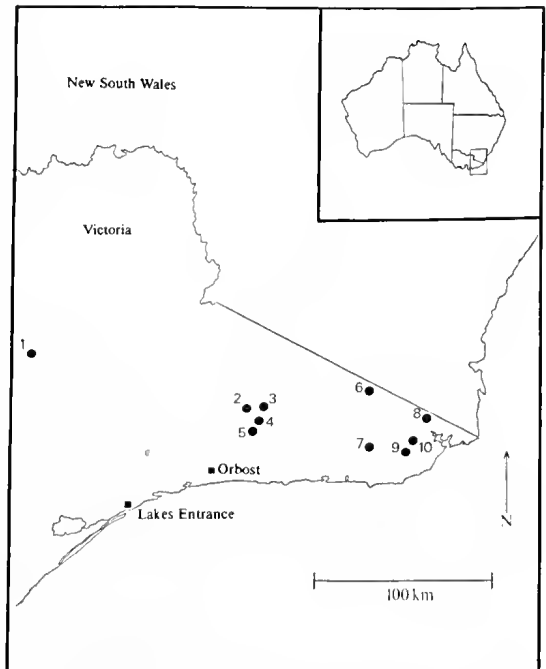
Fig. 1. Sites at which *Litoria phyllochroa* tadpoles were collected. Locality numbers refer to Table 1.

Date	Location & Aust. Map Grid	Micro-habitat	Museum Reg. No.	BL mm	TL mm	Gosner Stage	Water °C	Sympatric Species
21/12/89	Wongungarra R. 8323/004921 (1)	CBW	D61730	5.7	14.8	29	19	*L. lesueuri*
			”	5.1	12.9	28		
			”	5.5	13.0	29		
			”	4.9	12.7	25		
		FS					13	
18/01/90	Wongungarra R. 8323/004921 (1)	CBW	Not Collected				22	*L. lesueuri*
	8323/005920 (1)	IBW	Not Collected				30	*L. lesueuri*
		ISP	Not Collected					
20/2/90	Wongungarra R. 8323/010938 (1)	CSP	D61728	11.5		42	19.5	
			”	11.9	31.6	40		
			”	12.5	32.4	41		
			”	12.0		42		
			”	12.6		42		
			”	13.6		42		
			”	13.2		42		
22/2/90	Wongungarra R. 8323/004921 (1)	CBW	D61727	11.8	31.3	37	19.5	*L lesueuri*
			D61726	11.6		46		
			”	9.9		46		
			D61729	12.5	30.2	37		
			”	12.5	30.0	37		
			”	11.0	25.6	42		
			”	12.3	29.2	38		
			”	12.2	29.1	38		
			”	11.4	27.1	28		
			”	11.6	27.9	38		
22/2/90	Wongungarra R. 8323/005926 (1)	IBP	Not Collected				16.5	
22/12/90	Betka R. 8822/222434 (10)	CBW	Not Collected					
1/3/90	Yalmy R. 8523/276597 (3)	FS	D66040	12.4	28.3	39		*L. lesueuri*
			”	12.9	32.4	40		*L. citropa*
			”	12.9	22.4	41		*R. signifera*
			”	12.2	30.3	39		
			”	10.9	15.4	40		
8/1/91	Cann R. East Br. 8723/919818 (6)	CBW	D66039	11.5	28.3	40		*L. lesueuri*
			”	10.1	23.8	37		*L. citropa*
			”	10.5	25.2	38		*R. signifera*
			”	13.0	29.3	40		
			”	11.4	27.5	39		
21/1/91	Hard to Seek Ck 8822/256361 (7)	CBW	D66037	8.0	18.4	30		*L. peroni*
			”	9.2	21.5	35		*L. lesueuri*
			”	10.6	26.3	37		
			”	8.2	19.7	30		
			”	10.1	10.1	47		
15/2/91	Martins Ck 8623/424613 (4)		D66041	11.5	26.1	39		*L. lesueuri*
			”	11.5	26.4	38		
			”	11.5	27.6	39		
			”	10.9	25.6	39		
			”	11.6	27.1	39		
		FS	”	11.8	25.3	38		
			”	11.2	25.8	38		
			”	11.1	24.5	37		
			”	12.1	27.6	39		
			”	11.0	23.9	37		

Date	Location & Aust. Map Grid	Micro-habitat	Museum Reg. No.	BL mm	TL mm	Gosner Stage	Water °C	Sympatric Species
26/2/91	Sardine Ck 8522/280450 (5)	FS	D66042	8.6	18.8	32		*L. lesueuri*
			"	11.9	23.7	37		*L. citropa*
			"	11.8	31.4	41		*R. signifera*
			"	10.5	25.2	36		
			"	12.2	28.4	37		
			"	11.8	27.8	38		
28/1/92	Sardine Ck 8622/356482 (5)	FS	D66043	11.2	25.5	31		*L. citropa*
			"	11.4	26.5	36		*L. lesueuri*
			"	9.1	19.1	30		
			"	11.4	25.3	36		
			"	10.7	22.7	36		
11/3/91	Little Yalmy R. 8523/313612 (2)	FS	D66038	12.2	27.3	38		
			"	12.2	27.2	39		
			"	12.0	27.5	39		
			"	13.0	32.1	40		
			"	13.0	32.4	40		
12/1/92	Thurra R. 8723/035497 (7)	CSP	D66036	12.0	25.8	36		*L. citropa*
			"	10.9	26.4	36		*L. lesueuri*
			"	11.7	26.4	36		
			"	9.4	21.3	31		
			"	10.2	20.9	31		
			"	11.6	27.0	35		
			"	9.2	9.8	46		
			"	10.1	14.6	45		
20/3/92	Maramingo Ck 8823/327586 (8)	CSP	D66044	14.0	32.8	38		
			"	13.5	33.3	41		
			"	13.2	31.0	37		
			"	12.9	30.3	41		
			"	12.6	31.5	38		

Table 1. Localities, habitats, collection dates, measurements and Museum of Victoria registration numbers for tadpoles of *Litoria phyllochroa* examined in this study. Abbreviations for habitats are: CSP = connected streamside pool, ISP = isolated streamside pool, CBW = connected back-water of main stream, IBW = isolated back-water of main stream, IBP = isolated bedrock pool, FS = flowing stream. BL = body length, TL = total length. Numbers in parentheses refer to localities in Fig. 1.

the stream and surrounding vegetation also was made. Observations of tadpoles and activity of adult *L. phyllochroa* were made at additional sites in East Gippsland between October 1989 and January 1992.

Collected tadpoles were identified by growing them to metamorphosis. A series of tadpoles from each site was preserved in 10% formalin. Measurements of body and tail length were recorded using vernier callipers measuring to the nearest 0.1 mm (Table 1). Material examined has been lodged in the Museum of Victoria, Melbourne (NMV).

Descriptions of tadpoles were made by observation under a binocular dissecting microscope. Terminology follows Altig (1970) and Hero (1990). Developmental stages are those of

Gosner (1960). A single representative specimen (stage 37, NMV D61727) was illustrated by tracing from photographs. The labial tooth row formula (LTRF) illustrated is based on observations of several specimens at stages 25 to 42. The drawings depict melanic patterns that persist in preserved specimens (10% formalin). Habitat and life history notes also are presented to assist identification, but these are intended as a guide only and tadpoles could be found in different habitats and seasons than those given. Caution should be taken with descriptions of colour, as colour is often a function of water clarity (Bragg 1957).

Comparisons with tadpoles of other lotic species were made from descriptions in the literature and from specimens of *L. citropa, L.*

lesneuri and *L. spenceri* tadpoles collected during this study (Table 2). Measurements of body length and oral disc width of eight *L. spenceri* specimens were made with vernier callipers and compared with those of eight *L. phyllochroa* tadpoles at similar Gosner stages, using Student's t test.

RESULTS AND DISCUSSION

Description of tadpole (stage 37)

The anus is dextral and the spiracle sinistral. The body is elongated and flattened. The tail is moderately thick, has a rounded tip and is deepest in the anterior half. Neuromast pores are visible along the body and anterior section of the tail. The lateral lines may be heavily pigmented along part of their length and interspersed with unpigmented sections, but this varies considerably between individuals. Eyes are dorsolateral and the mouth is ventral. The nares are dorsal in position and directed anterolaterally. They are slightly closer to the tip of the snout than to the eyes, and spaced more closely than the eyes.

The mouth is ventral. The oral papillae have a wide anterior gap. Submarginal papillae are present beside the posterior and lateral oral papillae (Fig. 2). There are two rows of labial teeth in the anterior labium and three in the posterior labium. Median gaps are present in the second anterior and the first posterior tooth rows (Fig. 2). When preserved, the second anterior tooth rows commonly overlap at the middle.

The body is dark brown above with scattered fine silver chromatophores. The orbital and narial regions are paler with less uniform pigmentation. Large irregularly-shaped golden flecks are visible in live specimens on the flanks and extending onto the margins of the grey ventral surface. These melanophores turn black in preserved specimens. A few scattered melanophores are present on the venter of some individuals, where the intestine is visible. At later stages of development (> Gosner 35) dark spots may be present on the dorsal surface and may persist in preserved specimens. The tail muscle is pale with scattered melanophores forming small clumps or striations, with larger clumps along the dorsal edge. The fins are transparent with scattered melanophores, often in small clumps, becoming less numerous ventrally and anteriorly.

Tadpoles vary in total length from 12.7 mm at stage 25 to a maximum size recorded of 33.3 mm at stage 41 (Table 1). Snout–vent measurements taken of two newly metamorphosed individuals in the field and five reared in captivity ranged from 10.5 mm to 14.1 mm. Newly metamorphosed individuals are grey-brown with no green markings; the pale lateral zone typical of adults is visible. Captive individuals developed green pigmentation seven to fourteen days after metamorphosis.

Comparison

The tadpole of *L. phyllochroa* is morphologically similar to other described tadpoles of the *L. citropa* complex, including those of *L. spenceri*. It could also be confused with *L. lesneuri* in the field. Examination of the mouth parts of preserved specimens clearly distinguishes *L. lesneuri* and *L. citropa* from *L. phyllochroa*, *L.*

Species	No. Indiv.	Date	Aust. Map Grid	Museum Reg. No.
L. citropa	1	23/3/92	8823/281521	D66029
L. citropa	8	8/1/91	8723/898705	D66030
L. citropa	5	9/1/91	8622/356479	D66031
L. citropa	3	8/1/91	8723/919818	D66032
L. citropa	3	12/1/91	8723/035479	D66033
L. citropa	11	21/1/92	8822/256361	D66034
L. citropa	1	28/1/92	8622/356482	D66035
L. lesueuri	1	28/1/92	8622/356482	D66045
L. lesueuri	2	23/6/91	8523/156510	D66046
L. lesueuri	1	22/1/92	8822/223434	D66047
L. spenceri	1	25/2/92	8123/153622	D66048
L. spenceri	2	23/2/92	8122/385473	D66049
L. spenceri	3	10/3/92	8324/346276	D66050
L. spenceri	5	5/3/92	8324/339292	D66051

Table 2. Localities and Museum of Victoria registration numbers for tadpoles of *Litoria citropa*, *L. lesueuri* and *L. spenceri* examined in this study.
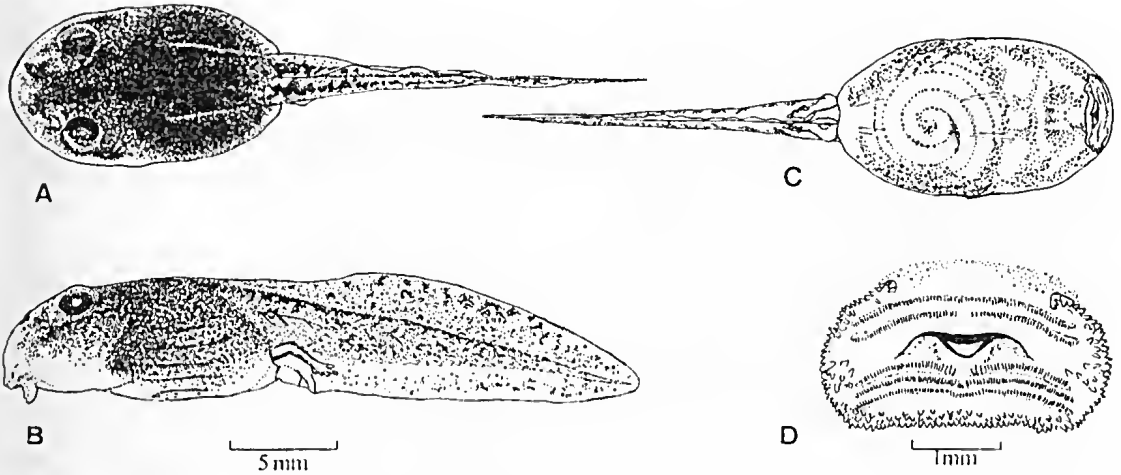
Fig. 2. *Litoria phyllochroa* tadpole (NMV D61727, stage 37). A, dorsal view. B, lateral view. C, ventral view. D, oral disc.

pearsoniana and *L. spenceri*. The first two species have a complete papillary border whilst the last three have a wide anterior gap in the oral papillae (Hero et al. in prep., McDonald & Davies 1990). *L. subglandulosa* is distinguished from all of the above species by the possession of a specialized mouth which contains no tooth rows and a small unpigmented beak (Tyler & Anstis 1975).

In life *L. lesueuri* is distinguished from species of the *L. citropa* complex by the large oral disc, yellowish tail fins with either no pigmentation or a few scattered chromatophores (personal observation), heavily pigmented tail muscle (Martin et al. 1966) and gold venter. *L. phyllochroa* has dark pigment scattered over the dorsal and ventral tail fins and a transparent venter. *L. citropa* may be distinguished from *L. phyllochroa* by the strong banding in the tail muscle pigmentation (Tyler & Anstis 1975) and by the presence of patches of dark pigmentation scattered over the tail fins.

The only described character of the tadpole of *L. pearsoniana* which appears to distinguish it from *L. phyllochroa* is the depth of the fin. McDonald & Davies (1990) noted that the fin of *L. pearsoniana* is deepest posteriorly, whereas in all specimens of *L. phyllochroa* examined during the present study the fin was deepest anterior to the midpoint of the tail.

Key to tadpoles of presently described species of the *L. citropa* complex and other lotic hylid tadpoles in Victoria

* = Ratio of body length to oral disc width

1.	Tooth rows present 2
—	Tooth rows absent ....,......*L. subglandulosa*
2.	Complete papillary border 3
—	Wide anterior gap in papillary border 4
3.	Heavily pigmented banding of tail muscle but little or no pigmentation in fins. Heavily pigmented venter obscuring intestine ....*L. lesueuri*
—	Melanic clumps in fins, intestine clearly visible through venter ....*L. citropa*
4.	Fin deepest anterior to midpoint of tail 5
—	Fin deepest posteriorly ....*L. pearsoniana*
5.	Small oral disc (BL/ODW > 3.8*). Clear venter .....*L. phyllochroa*
—	Large oral disc (BL/ODW < 3.8*). Dark pigmentation extending onto venter, partially obscuring intestine ....*L. spenceri*

Comparison of oral disc width to body length ratios of preserved *L. spenceri* and *L. phyllochroa* tadpoles indicates that *L spenceri* has a significantly wider oral disc (t = 7.426, P < 0.005; Table 3). In addition, the oral disc of *L. spenceri* is darkly pigmented and has thicker papillae. Preserved specimens of *L. phyllochroa* have few melanophores on the venter and the intestine is clearly visible, whilst the intestine of *L. spenceri* is largely obscured by dark melanophores (Hero et al. in prep.). This distinction is not visible in life as both species appear to have a transparent venter. However, the absence of large golden flecks on the flanks of *L. spenceri* tadpoles is a distinction from *L. phyllochroa* and assists identification in the field.

Habitat

Litoria phyllochroa tadpoles were found in a variety of micro-habitats in eastern Victoria (Table 1) including isolated and connected streamside pools, the main channel of streams, along shingle banks and in large back-waters. Tadpoles were often found in different situations along the one stream. For example, on the Wongungarra River tadpoles were found in isolated and connected streamside pools on shingle banks, in large back-waters of the river and in the main stream. Along Sardine Creek, tadpoles were found at one location in cattle hoof prints along a sand bar. Substrate included rock, gravel, fine sand and rotting litter. Tadpoles were most frequently found in the quieter sections of streams, such as deep pools, or amongst pebbles along shingle banks. Tadpoles were generally found on the bottom, either on rocks or amongst litter where they appeared to be feeding on an accumulated mixture of silt, detritus and algae.

	L. phyllochroa	L. spenceri
	3.9	3.1
	4.0	3.2
	4.0	3.2
	4.3	3.4
	4.3	3.5
	4.4	3.5
	4.4	3.5
	4.5	3.7
mean	4.2	3.4
SD	0.23	0.20

Table 3. Body length to oral disc width ratios for samples of *Litoria phyllochroa* and *L. spenceri* tadpoles between Gosner stages 33 and 38.

Fine grains of sand are clearly visible in the intestines of preserved specimens.

Collection sites ranged in altitude from near sea level on Hard To Seek Creek to 700–800 m along the Wongungarra River. The calibre of stream varied markedly, from small, slow-flowing creeks, such as Martins Creek, to major rivers with heavy flows, such as the Wongungarra and Yalmy rivers.

Tadpoles were found along streams flowing through a range of vegetation communities. These included warm temperate rainforest (Thurra River) and *Tristaniopsis laurina*-dominated riparian forest (Sardine Creek), riparian scrub-heathland dominated by *Melaleuca squarrosa* (Hard To Seek Creek), and a range of open eucalypt forest communities, including dry sclerophyll and wet sclerophyll forests (Cann River and Martins Creek respectively).

At a number of sites fish (salmonid or galaxiid species) were observed swimming among *L. phyllochroa* tadpoles. Salmonid species are present in all of the stream systems in which *L. phyllochroa* was found, except the Betka River and Hard To Seed Creek (Raadik in prep.). Tadpoles were recorded in the main channels of both of the latter streams which are known to include twelve species of native fish in their catchments (Raadik in prep.). This suggests that *L. phyllochroa* tadpoles have mechanisms for defence against predation by both native fish and introduced salmonid species.

Sympatry

Five other species of tadpoles were found along streams at the same time as *L. phyllochroa* tadpoles were collected, namely *L. citropa, L. lesueuri, L. peroni, L. spenceri* and *Ranidella signifera*. With the exception of the Little Yalmy River and Maramingo Creek, *L. lesueuri* tadpoles were found at all locations, both in syntopy (i.e. in the same waterbody) and in sympatry (different waterbody, same section of river). *Litoria citropa* tadpoles were found in both syntopy and sympatry with those of *L. phyllochroa* and *L. lesueuri* in Sardine Creek and in the Cann and Yalmy rivers. *Litoria peroni* tadpoles were found in syntopy with *L. phyllochroa* only in Hard To Seek Creek. *L. peroni* usually utilizes stationary water bodies for reproduction (personal observation) and is not considered a lotic species in this study. *Litoria spenceri* tadpoles were only found in sympatry with *L. phyllochroa* on the Wongungarra River, but metamorphling *L.phyllochroa, L.spenceri* and *L. lesueuri* have

been found together on Snowy Creek, north-east Victoria (G. Johnson pers. comm., Department of Conservation & Environment, Wodonga, Victoria). Tadpoles of *Ranidella signifera* were found in sympatry with those of *L. phyllochroa* on the Cann, Betka and Yalmy rivers and on Sardine Creek.

Breeding activity

The breeding activity and stream habitats used by *L. phyllochroa* are generally similar to those of other species within the *L. citropa* complex and appear to parallel closely those of *L. pearsoniana* (Tyler & Anstis 1975, McDonald & Davies 1990).

In 1989/1990 and 1990/1991 males were heard calling in East Gippsland between early October and February. In 1991 and 1992 males were heard calling at one location as late as mid-April and as early as mid-September. Males are regularly heard calling during the day, although calling is more intense in the evenings. Calling activity is most intense in October and November, during or after rain. Males were most frequently observed calling from grass and *Lomandra longifolia* tussocks adjacent to the stream and from small over-hanging branches or fern fronds up to 2.5 m above the stream.

Tadpoles were encountered in mid-December at stages 25–29 (Table 1). Newly metamorphosed individuals were recorded between mid-February and late March. However, tadpoles at stages 30–40 were also observed in some streams in late March. Given a peak in breeding activity in October/November and the presence of tadpoles in late March, larval development may take between three and six months.

Adult behaviour

Litoria phyllochroa is active both during the day and at night. In January 1991 several individuals were found hopping amongst ground ferns in warm temperate rainforest along Martins Creek (dry temperature 20°C) and in a grassy clearing at mid-day (dry temperature 26°C). Individuals were also observed basking on small branches over the Yalmy River, Thurra River and Maramingo Creek (dry temperature 16–24°C). These individuals had taken on dark olive and almost black colorations.

In spring and summer adult male frogs were found sheltering near the banks of streams under rocks and amongst dense ground vegetation. In March and April several individuals were collected from amongst leaf and bark litter at the bases of large trees in damp sclerophyll forest at sites up to 200 m from the stream.

Litoria phyllochroa exhibits some activity during the winter period. In July 1991, 12 individuals were found perched on small branches, *Gahnia* spp. and fern fronds in warm temperate rainforest along the Thurra River at night (temperature 8°C, 100% humidity).

ACKNOWLEDGEMENTS

REFERENCES

ALTIG, P.., 1970. A key to the tadpoles of the continental United States and Canada. *Herpetologica* 26: 180–207.

BRAGG, A. N., 1957. Variations in colors and color patterns in tadpoles in Oklahoma. *Copeia* 1957: 36–39.

BROOK, A. J., 1983. Atlas of Australian Anura. Department of Zoology, University of Melbourne, Publication No. 7.

COPLAND. S. J., 1957. Australian tree frogs of the genus *Hyla. Proceedings of the Linnean Society of New South Wales* 82: 9–108.

GOSNER, K. L., 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16: 183–190.

GUNTHER, A., 1863. Observations on Australian treefrogs in the Society's menagerie. *Proceedings of the Zoological Society of London* 1863: 249–251.

HERO, J.-M., 1990. An illustrated key to tadpoles occurring in the central Amazon rainforest, Manaus, Amazonas, Brasil. *Amazoniana* 11: 201–262.

HERO, J.-M., LITTLEJOHN, M, J. & MARENTELLI, J., 1991. *Frogwatch Field Guide to Victorian Frogs.* Department of Conservation and Environment Victoria, Melbourne, 108 p.

HERO, J.-M., WATSON, G. F. & GILLESPIE, G. R., in prep. The tadpole of *Litoria spenceri* (Anura: Hylidae).

LITTLEJOHN, M. J., 1967. Patterns of zoogeography and speciation in south-eastern Australian amphibia. In *Australian Inland Waters and their Fauna*, A. H. Weatherly, ed., Australian National University Press, Canberra, 150–174.

MARTIN, A. A., LITTLEJOHN, M. J. & RAWLINSON, P. A., 1966. A key to the anuran eggs of the Melbourne area, and an addition to the anuran fauna. *Victorian Nauralist* 83: 312–315.

MCDONALD, K. R. & DAVIES, M., 1990. Morphology and biology of the Australian tree frog *Litoria pearsoniana* (Copland) (Anura: Hylidae). *Transactions of the Royal Society of South Australia* 114: 145–156.

RAADIK, T. A., in prep. *Aquatic Biological Resources of East Gippsland: Fish and Macro-Invertebrates*. Silicultural Systems Project Technical Report Series, Department of Conservation and Environment, Victoria.

TYLER, M. J., 1992. *Encyclopedia of Australian Animals: Frogs*. Angus & Robertson, Sydney, 109 p.

TYLER, M. J. & ANSTIS, M., 1975. Taxonomy and biology of frogs of the *Litoria citropa* complex (Anura: Hylidae). *Records of the South Australian Museum* 17: 41–50.

TYLER, M. J. & DAVIES, M., 1978. Species groups within the Australopapuan hylid frog genus *Litoria* Tschudi. *Australian Journal of Zoology Supplementary Series* 63: 1–79.

TYLER, M. J, & DAVIES, M., 1985. A new species of *Litoria* (Anura: Hylidae) from New South Wales, Australia. *Copeia* 1985: 145–149.

WATSON, G. F., LITTLEJOHN, M. J., HERO, J.-M. & ROBERTSON, P., 1991. *Conservation Status, Ecology and Management of the Spotted Tree Frog* (Litoria spenceri). Arthur Rylah Institute for Environmental Research Technical Report Series No. 116, Department of Conservation and Environment, Victoria, 40 p.

A NEW GENUS OF BRISSID ECHINOID FROM THE UPPER OLIGOCENE OF VICTORIA

K. J. McNamara

Department of Earth and Planetary Sciences, Western Australian Museum, Francis Street, Perth, Western Australia 6000

McNamara, K. J., 1993:03:31. A new genus of brissid echinoid from the Upper Oligocene of Victoria. *Proceedings of the Royal Society of Victoria* 105 (1): 39–48. ISSN 0035-9211.

A new genus and species of brissid heart urchin, *Apoxypetalum chenjafra* sp. nov., is described from the Late Oligocene Waurn Ponds Limestone at Waurn Ponds, Victoria. This small heart urchin is particularly characterised by the reduction in size of the ambulacral plates in the vicinity of the apical system. The echinoid fauna of the predominantly Late Oligocene Jan Juc Formation, within which the Waurn Ponds and Point Addis Limestones occur, is documented. The Waurn Ponds Limestone is shown to contain a spatangoid biofacies, the Point Addis Limestone a cassiduloid/clypeasteroid biofacies, and the rest of the Jan Juc Formation mixed spatangoid and clypeasteroid biofacies. Biofacies differences are considered to be due to variations between the units in sediment grain size, reflecting, in part, differences in depths of deposition.

THE WAURN PONDS Limestone is a 10 m thick sequence of predominantly bryozoal calcarenites that outcrops in a series of quarries along monoclinal structures at Waurn Ponds, west of Geelong in Victoria. This limestone occurs in the easternmost part of the Torquay Basin and is a member of the Jan Juc Formation, a predominantly Late Oligocene unit (Janjukian Stage, planktic foraminiferal zone 22) though the uppermost part is of earliest Miocene age (Abele 1976). The Jan Juc Formation is predominantly a glauconitic marl interbedded with sandy glauconitic calcarenite. Locally, bryozoal calcarenite-rich units are present, such as the Waurn Ponds Limestone and the Point Addis Limestone.

Fossil echinoids have long been known from the bryozoal calcarenites of the Waurn Ponds Limestone, McCoy (1882) having described *Pericosmus nelsoni* from a nodular limestone band near the base of the limestone. This species has more recently been placed into a separate genus named *Waurnia* by McNamara & Philip (1984). Intensive collecting at Waurn Ponds in the last few years, mainly by Chris Ah Yee and Janice Krause but also by Frank and Enid Holmes, has yielded a relatively diverse and distinctive echinoid fauna dominated by spatangoids. These collections have been made principally from the "Old Pit", to the west of the current quarry area (Fig. 1). This pit is the original pit of modern day workings and is distinct from the nineteenth century quarries from which McCoy (1882) obtained his material. On the basis of some of the material collected by Chris Ah Yee, McNamara et al. (1986) redescribed *Granobrissoides australiae* (Cotteau). Other echinoids recently described or newly recorded from the Waurn Ponds Limestone are *Eupatagus collabus* Kruse & Philip, 1985, *Protenaster philipi* McNamara, 1985 and *Meoma tuberculata* Hutton (McNamara et al. 1986). The last species was previously known only from Early Oligocene strata in South Australia.

Recent collecting has focused on the basal part of the Waurn Ponds Limestone in the "Old Pit". The echinoids that have been discovered reinforce the rather unusual nature of the echinoid fauna by revealing another undescribed genus. Two of the other genera, *Waurnia* and *Granobrissoides*, are restricted to this unit. Unlike the coarse bryozoal nature of most of the Waurn Ponds Limestone, the basal part is a thin (less than 1 m), fine-grained calcarenite that also contains a lithic and glauconitic fraction. It occurs about 1.2 m below the bed within which *Waurnia nelsoni* has been found (McCoy 1882, Gill 1952). In addition to the new genus, which is represented by some 38 individuals, rare specimens of *Hemiaster verecundus* McNamara, 1987 and *Brissopsis* sp. have also been found in the basal bed (Chris Ah Yee, pers. comm.). This brings to 15 the number of echinoid species collected from the Waurn Ponds Limestone (Table 1, Fig. 5), though some of these species have not previously been recorded from the unit.

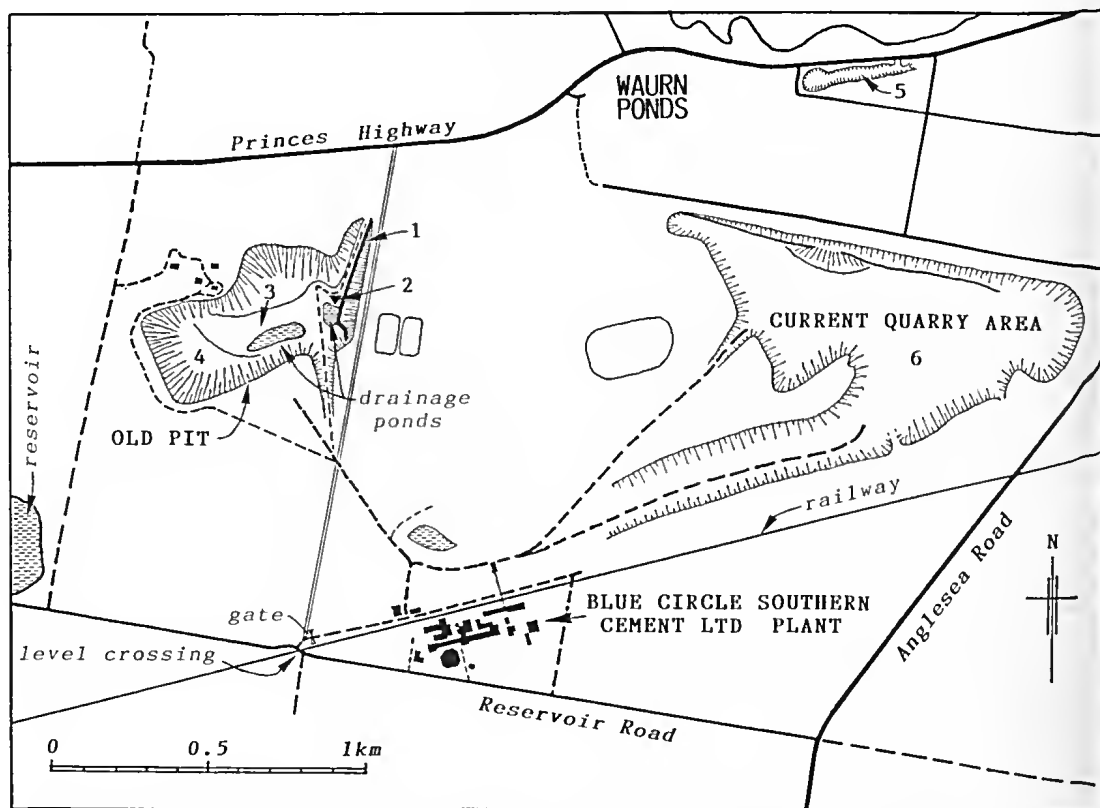The material on which this study is based is

Fig. 1. Map showing location of quarries in the Waurn Ponds Limestone from which *Apoxypetalum chenjafra* and other echinoids have been collected. Map drawn by Mr Frank Holmes and based on January 1990 aerial photograph (Division of Survey and Mapping, Department of Property and Services, Victoria). 1, vertical cut along line of monocline (*Waurnia nelsoni* bed bottom 1 m of cut). 2, section of basal bed of quarry, immediately east of vertical cut, from which majority of specimens of *Apoxypetalum chenjafra* were collected. 3, base of quarry, sloping south to drainage pond, containing occasional echinoids including *Apoxypetalum chenjafra*, 4, area of quarry yielding most echinoids, in particular *Corystus dysasteroides*, immediately above an ironstone band about a quarter of the way up the slope. 5, old lime quarry and kiln, probably the quarry referred to by McCoy (1882) as the type locality of *Waurnia nelsoni*. 6, currently worked pit.

housed in the collections of the Western Australian Musuem, Perth (WAM) and the Museum of Victoria, Melbourne (NMV).

SYSTEMATIC PALAEONTOLOGY

Order Spatangoida Claus, 1876
Family Brissidae Gray, 1855

Genus Apoxypetalum gen. nov.

Etymology. From the Greek *apoxys* and *petalon*, referring to the reduced nature of the anterior petals. Gender neuter.

Type species. Apoxypetalum chenjafra sp. nov.

Diagnosis. Test cordate, with shallow anterior notch. Apex mid-test length, posterior to apical system which is about one-third test length from anterior. Ethmolytic, with 4 gonopores. Petals short and sunken adambitally but flush with test surface adapically; anterior petals almost transverse. Anterior poriferous row of anterior petals (IIb and IVa) with a greater number of smaller plates and more reduced pore pairs than posterior row. In both rows pore pairs fail to reach apical system, occurring only on distal parts of petals. In posterior petals inner and outer rows with equal number of reduced plates and pore pairs. Peripetalous fasciole very narrow; subanal fasciole very wide. Peristome subcentral.

Echinoid species	Waurn Ponds Lst.	Point Addis Lst.	Jan Juc Fm.
Goniosigma murrayensis	—	1	—
Ortholophus woodsi	—	4	2
Zenocentrotus peregrinus	—	1[1]	—
Corystus dysasteroides	5	1	2
Echinolampas curtata	10	—	—
Australanthus florescens	6	36	—
Apatopygus sp.	—	1	—
Fibularia gregata	—	1	15
Willungaster scutellaris	10	23	25
Monostychia sp.	1	6	1
Hemiaster verecundus	2	—	—
Protenaster philipi	5	—	—
Waurnia nelsoni	15	—	—
Eupatagus wrighti	—	3	40
Eupatagus collabus	2	—	—
Brissopsis sp.	0.5	1	1
Granobrissoides australiae	6	—	—
Lovenia forbesii	2	22	15
Meoma tuberculata	0.5	—	—
Pericosmus maccoyi	0.5	—	—
Apoxypetalum cheujafra	34	—	—
	n = 196[2]	n = 105[2]	n = 83[3]

Table 1. Echinoid species found in the Late Oligocene strata of the Torquay Basin. Data presented as percentages of the total numbers of specimens found in each formation, based on collections held in the Western Australian Museum. [1]Only the holotype, described by Philip (1965), is known. [2]Based on specimens collected by C. Ah Yee and K. J. McNamara. [3]Based on specimens collected by K. J. McNamara.

Plastron with prominent keel, particularly posteriorly.

Remarks. Of brissids with an anteriorly positioned apical system and transverse anterior petals, *Apoxypetalum* bears a superficial similarity to *Brissus* but can be distinguished from that genus by its small size, the presence of an anterior notch, the shorter petals, the anterior petals that are only poriferous distally, the peripetalous fasciole that is not indented between the petals, the flatter adoral surface and the subcentral peristome. *Anabrissus*, which closely resembles *Brissus*, has a weak peripetalous fasciole like *Apoxypetalum* but has only three gonopores. *Apoxypetalum* is similar to the small, late Cretaceous to early Palaeocene *Diplodetus (Protobrissus)*; however, *Apoxypetalum* can be distinguished by its well developed subanal fasciole, more strongly vaulted test and incompletely poriferous petals (see Mortensen 1951, fig. 176).

Apoxypetalum is not unlike *Migliorinia*, from the Eocene of Somalia, but *Apoxypetalum* has shorter, much narrower petals and a more vaulted test, and in *Migliorinia* the pore pairs are not reduced adapically. The only brissid that

has reduced pore pairs near the apical system is *Brissopsis*, but that genus has reduced pores only in the anterior row of the anterior petals (ambulacra IIb and IVa) and in the posterior row of the posterior petals (ambulacra Ia and Vb); furthermore, it lacks the anteriorly positioned apical system and consequent transversely orientated anterior petals. Some species of *Macropneustes*, such as *M. minor* (Agassiz) from the Eocene of France, bear a superficial similarity to *Apoxypetalum*, but the new genus can be distinguished not only on the nature of the pore pair size in the petals but also in its much shorter petals and the absence of any large tubercles on the aboral surface of the test.

Amongst Australian spatangoids, *Apoxypetalum* is similar to the Miocene marsupiate genus *Peraspatangus*. Both genera share an anteriorly positioned apical system, transverse petals that adapically have reduced pore pairs, a keeled plastron and relatively posteriorly positioned peristome. However, *Peraspatangus* lacks a peripetalous fasciole and consequently was placed in the Spatangidae by Philip & Foster (1971). *Apoxypetalum* can further be distinguished by its anterior notch, sunken petals and absence of a marsupium in the females. *Apoxypetalum* is also

superficially similar to the Australian spatan-
goid *Spatagobrissus* (see McNamara et al. 1986)
but can be distinguished by its smaller aboral
tuberculation, sunken petals, anterior notch,
larger peristome and flatter adoral surface.

Apoxypetalum chenjafra sp. nov.

Figs 2–4

Holotype. NMV P135991 (Fig. 2A–D), from the Jan-
jukian (Late Oligocene) Waurn Ponds Limestone,
Blue Circle Southern Cement Quarry, Reservoir
Road, Waurn Ponds, Victoria (Geelong 1:25,000 top-
ographic map 7721-1-3, grid reference BT 603666).
The quarry is situated between the Princes Highway
and Reservoir Road, 1 km north-west of BCSC build-
ings. The specimen was collected from the basal bed of
the Waurn Ponds Limestone at the north-eastern end
of the quarry (see Fig. 1).

Other material. Paratypes NMV P135989, P135990,
P135992, P135993 and WAM 92.374–382 from the
same horizon and locality as the holotype. A further 24
incomplete specimens were also collected: WAM
90.266–268, 90.269 (7 specimens), 91.8, 91.11, 92.383
(12 specimens).

Etymology. An arbitrary combination of letters taken
from the first names of the four collectors of the speci-
mens, respectively *Ch*ris Ah Yee, *En*id Holmes, *Ja*nice
Krause and *Fra*nk Holmes. Consequently the species
name is pronounced "ken-ja-fra". The name should be
considered as a noun in apposition.

Diagnosis. As for genus.

Description. Test small, reaching a maximum
known test length (TL) of 23.5 mm; cordate,
with shallow anterior notch; highest in inter-
ambulacrum 5 (Fig. 3D), near mid-test length
(between 47% TL and 56% TL from anterior
ambitus), height 54–62% TL; test widest just an-
terior to mid-test length but posterior to apical
system, maximum width 90–98% TL. Aboral
surface strongly convex, declining steeply anter-
iorly; posteriorly truncated, interambulacrum 5
slightly overhanging periproct. Apical system
anterior to centre, 35–41% TL from anterior
ambitus; ethmolytic, with four genital pores.
   Ambulacrum III shallow on aboral surface;
narrow adapically, progressively broadening ad-
ambitally; with up to 12 very small pore pairs;
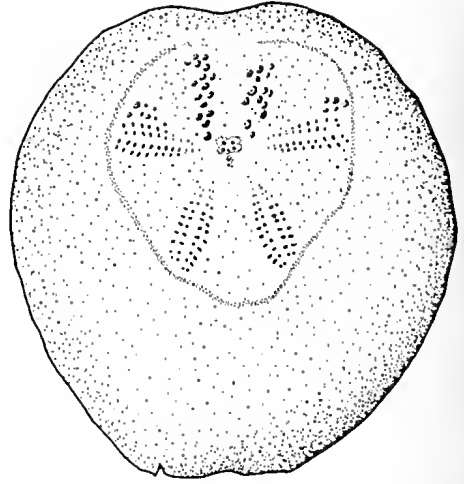pore pairs aligned obliquely almost exsagittally;

Fig. 2. Camera lucida drawing of aboral view of *Apoxy-
petalum chenjafra*, WAM 91.9. Bar represents 5 mm.

not conjugate. Anterior petals shallow; narrow,
width 7–8% TL; almost transverse, diverging an-
teriorly at about 160°; short, 22–27% TL; pores
circular to ovoid, not conjugate; 12–14 pore
pairs in anterior row (ambulacra IIb and IVa);
11–15 in posterior row (ambulacra IIa and IVb);
in anterior row, abapical 5–7 pore pairs large,
adapical 5–7 pore pairs very reduced in size; in
posterior row larger pore pairs are more numer-
ous, abapical 8–10 being large whereas adapi-
cally only 3–5 are reduced in size. Pore pairs fail
to reach apical system (Figs 2, 3N, 4). Posterior
petals shallow and same width as anterior petals;
usually same length as anterior petals but in two
individuals they are shorter (22% TL compared
with 26% TL); total variation in length is 21–
27% TL; 11–15 pore pairs in each row, fewer in
smaller than in larger specimens; unlike anterior
petals, rows bear roughly equal number of pore
pairs, 7–10 large pore pairs and 4–6 small ones.
Both anterior and posterior petals are only
sunken in region containing larger plates pierced
by larger pore pairs; adapical parts of petals with
smaller plates and small or absent pores not
sunken. Peripetalous fasciole very narrow (Fig.
2); only slightly indented between petal extremi-

Fig. 3. *Apoxypetalum chenjafra* gen. et sp. nov. A–D, holotype, NMV P135991, aboral, adoral, posterior and
lateral views. E, paratype, WAM 92.375, aboral view of specimen with spines. F, G, paratype, WAM 92.377,
aboral and lateral views. H, paratype, WAM 91.9, aboral view. I–K, N, paratype, WAM 92.374, adoral, lateral,
posterior and aboral views. L, M, paratype, NMV P135989, aboral and adoral views. All specimens from the
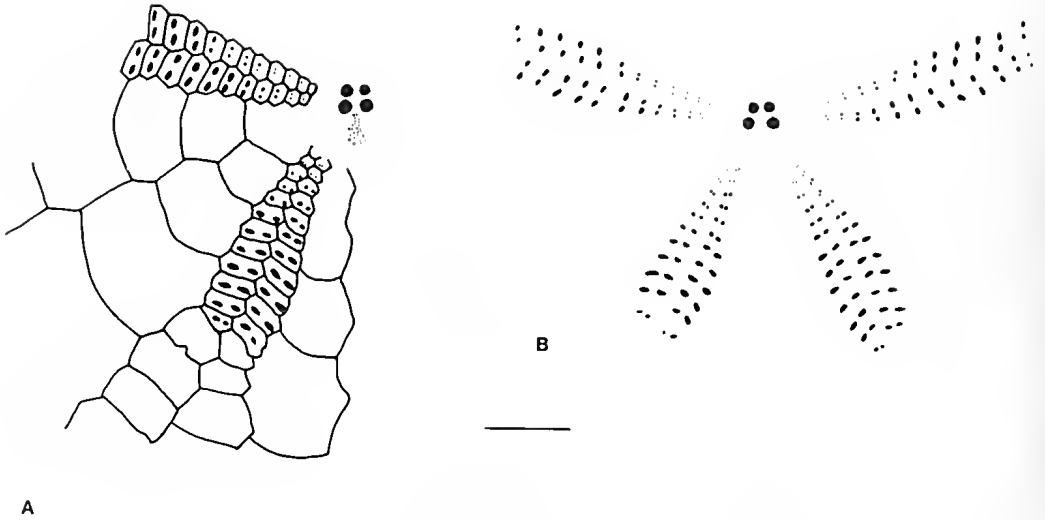Waurn Ponds Limestone, Waurn Ponds, Victoria. All × 2.
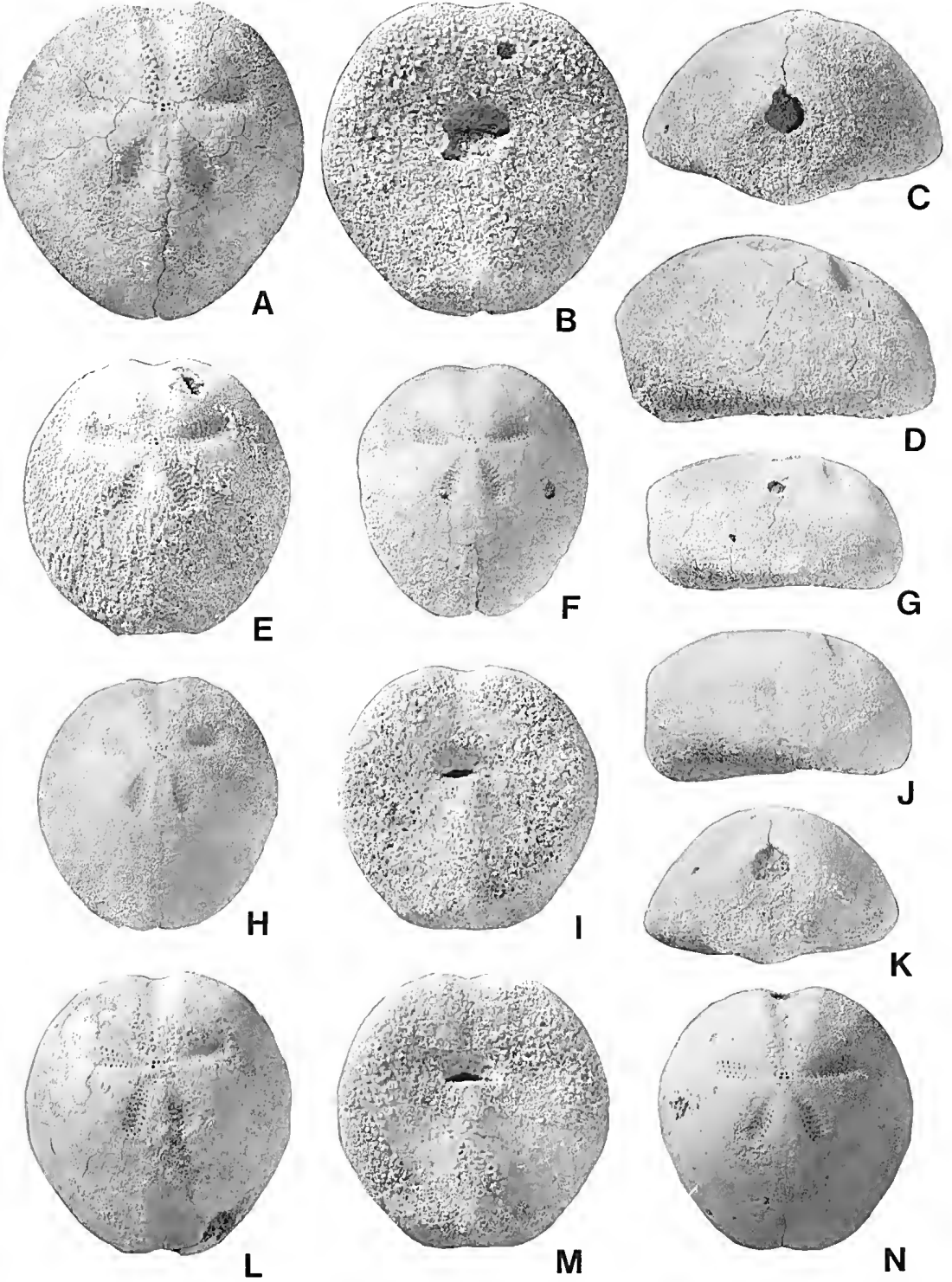
Fig. 4. Camera lucida drawings of part of the aboral surface of *Apoxypetalum chenjafra.* A, NMV P135989, part of aboral plating, apical system and pore pairs. B, WAM 92.374, genital pores and pore pairs, illustrating how the pore pairs fail to reach the apical system, and the reduction in pore pair size in the anterior row of the anterior petals. Bar represents 2 mm.

ties; crossing ambulacrum III close to apical system where anterior face of test plunges steeply to ambitus. Aboral tuberculation sparse, tubercles generally small, with diameter of about 0.15 mm; however, tubercles larger near petals and on flanks of ambulacrum III (Figs 2, 3A, H, L, N), with diameter of 0.4mm. In one specimen (WAM 92.375, Fig. 3E) some of the aboral spines are preserved. These are straight to slightly curved, never more than 2 mm long, and 0.1 mm wide.

Peristome relatively large (Fig. 3B, I, M), width 18–22% TL in adults; not sunken, situated subcentrally with anterior of labrum 40–43% TL from anterior ambitus; few specimens have well preserved adoral surfaces, nature of phyllodal pores thus unknown. Labrum short, about as long as wide; only slightly convex anteriorly. Plastron relatively narrow, gradually increasing in width posteriorly to width of 25% TL; with a sharp sagittal keel (Fig. 3C, K) which increases in intensity posteriorly. Periproct circular (Fig. 3K), with diameter of 12–14% TL. Adoral tuberculation sparse; tubercles relatively large, up to 0.7 mm in diameter, and crenulate.

Discussion. Apoxypetalum chenjafra can be distinguished from the other two, small echinoids that coexist with it in the basal part of the Waurn Ponds Limestone, namely *Hemiaster verecundus* McNamara, 1987 and *Brissopsis* sp., largely on the basis of its transverse anterior petals and anteriorly positioned apical system. It can further be distinguished from *H. verecundus* by its cordate test which is not so strongly vaulted posteriorly and by its narrower petals. It also differs from *Brissopsis* sp. in lacking adapically coalesced petals and in having a more vaulted test.

A number of specimens show evidence of having suffered predation, probably from cassid gastropods. McNamara (1990) reported the common occurrence of such predation in some Miocene spatangoids. Of specimens of *Apoxypetalum chenjafra* that are more than 75% complete, 38% (n = 16) show evidence of probably lethal predation in the form of a circular perforation in the test. These perforations, which range in diameter between 0.9 and 1.8 mm (mean = 1.3 mm), are located on the aboral surface in 66% of specimens (Fig. 3F, G), on the anterior ambitus (Fig. 3N) in 17% and on the adoral surface (Fig. 3B) in another 17%. This is the stratigraphically oldest reported evidence for gastropod predation on Australian echinoids.

LATE OLIGOCENE ECHINOID BIOFACIES OF THE TORQUAY BASIN

The Late Oligocene strata of the Torquay Basin outcrop predominantly in coastal cliff sections

in the vicinity of Torquay. The principal unit, the Jan Juc Formation, consists at its type locality at Bird Rock near Torquay of 9.8 m of olive grey and brownish grey silty, glauconitic marl, interbedded with clayey sandy glauconitic calcarenite (Abele 1976). In subsurface the unit reaches up to 88 m in thickness. The echinoid fauna discussed in this study was collected by the author at Fisherman's Steps and is represented by eight species (Table 1). It is dominated by spatangoids and clypeasteroids, which together comprise 76% of the echinoid fauna and 97% of the specimens collected (Table 2). More than half (65%) of the fauna comprises individuals of two species: the spatangoid *Eupatagus wrighti* and the clypeasteroid *Willungaster scutellaris*. Two further species, *Fibularia gregata* and *Lovenia forbesii*, make up a further 30%. Thus 95% of individuals of this echinoid fauna comprise just half of the total known species.

At Point Addis the Jan Juc Formation is represented by the Point Addis Limestone, a sandy bryozoal calcarenite more than 12 m thick (Abele 1976). The echinoid fauna is more diverse than that of the Jan Juc Formation (*sensu stricto*), being represented by 12 species (Table 1). The dominant group, comprising 37% of the fauna, is the cassiduloids, a group unknown in the Jan Juc Formation. Clypeasteroids and spatangoids together make up more than half of the remaining echinoid orders—30% and 26% respectively (Table 2)—this being almost half of the complement of these groups in the Jan Juc Formation. The dominant species in the Point Addis Limestone is the cassiduloid *Australanthus florescens*, individuals of which represent a third of the echinoid fauna. Apart from *Willungaster scutellaris* and *Lovenia forbesii*, the rest of the echinoids are rare elements of the fauna (Table 1). Thus a quarter of the echinoid species from the Point Addis Limestone are represented by 81% of the specimens collected. Of the total of 21 echinoid species known from the Upper Oligocene in the Torquay Basin, eight are shared by

the Jan Juc Formation and the Point Addis Limestone. Of these, only two species occur with some degree of frequency in both units: *Willungaster scutellaris* and *Lovenia forbesii* (Table 1). The most common species in the Point Addis Limestone, *Australanthus florescens*, is not known from the Jan Juc Formation, while *Eupatagus wrighti*, the dominant member of the Jan Juc Formation, is a rare element in the Point Addis Limestone.

The echinoid fauna of the Waurn Ponds Limestone (Fig. 5) is even more distinct from that of the Jan Juc Formation and the Point Addis Limestone than the echinoid faunas of these units are from each other. Of the 21 Late Oligocene species known from these three units only five are shared by the Waurn Ponds Limestone and the Point Addis Limestone, and only four with the Jan Juc Formation. Indeed, only four species occur in all three formations: *Corystus dysasteroides*, *Willungaster scutellaris*, *Brissopsis* sp. and *Lovenia forbesii*.

A distinctive feature of the Waurn Ponds echinoid fauna is the dominance of spatangoids, which comprise almost three-quarters of the echinoid fauna, both in terms of number of species and numbers of individuals (Table 2). In this respect the fauna is quite different from that of the Point Addis Limestone, which is dominated by cassiduloids and clypeasteroids. This is so even though both faunas inhabited similar sediments of relatively coarse bryozoal calcarenites. The Jan Juc Formation is somewhat intermediate in character, being a mixed spatangoid/clypeasteroid fauna. Another characteristic feature of the Waurn Ponds Limestone echinoid fauna is the high percentage of endemic genera, higher than for any other southern Australian Tertiary formation, the genera *Waurnia, Granobrissoides* and *Apoxypetalum* being known only from the Waurn Ponds Limestone.

Within the Waurn Ponds Limestone there are minor differences between the lower and upper beds. The lower beds (0–2 m) are dominated by

Echinoid orders	Waurn Ponds Lst.	Point Addis Lst.	Jan Juc Fm.
Regulars	—	6 (*25*)	2 (*12*)
Holasteroids	5 (*7*)	1 (*8*)	1 (*12*)
Cassiduloids	16 (*14*)	37 (*17*)	—
Clypeasteroids	11 (*7*)	30 (*25*)	41 (*38*)
Spatangoids	68 (*72*)	26 (*25*)	56 (*38*)

Table 2. Distribution of echinoid orders in the Late Oligocene strata of the Torquay Basin. Data presented as percentages of the total numbers of specimens and species (italics) found in each formation, based on collections in the Western Australian Museum.
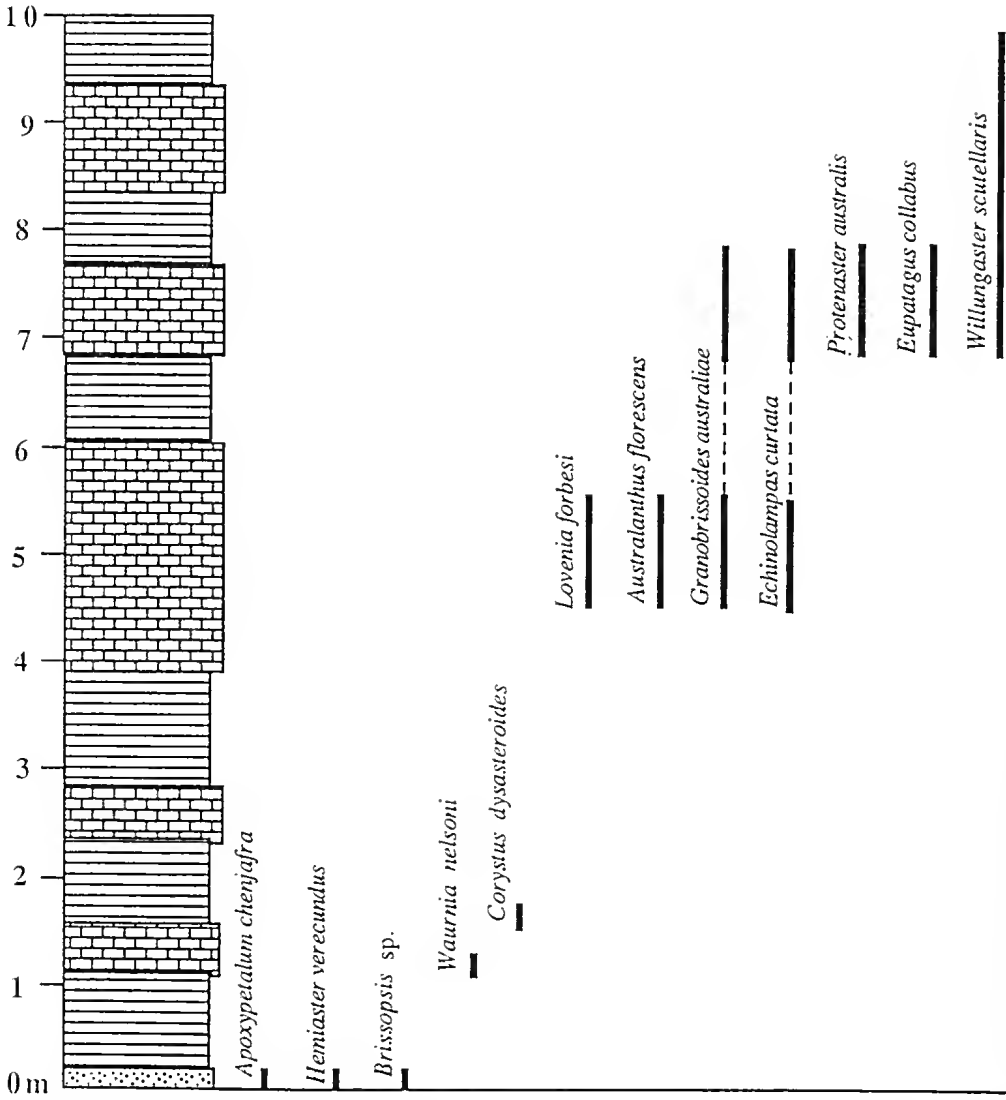
Fig. 5. Diagrammatic section through the Waurn Ponds Limestone in the "Old Pit", showing main fossiliferous horizons and distribution of echinoid taxa. Stippling represents basal sandy unit with *Apoxypetalum chenjafra*; horizontal parallel lines represent more marly horizons; brick pattern represents bryozoal calcarenite beds in which the echinoids occur. *Pericosmus maccoyi* and *Meoma tuberculata* are not included because their stratigraphic position in the section is not known.

spatangoids (four out of the five genera, the fifth being the holasteroid *Corystus*). *Apoxypetalum chenjafra*, which comprises 30% of the fauna, and *Waurnia nelsoni*, the next most common species in the Waurn Ponds Limestone (19%), are both found in the basal part of the Waurn Ponds section (Fig. 5). The upper beds (4–10 m) contain spatangoids, cassiduloids and a clypeas-teroid. But even here spatangoids are dominant, comprising four of the seven genera.

Analysis of the echinoid faunas of southern Australia (McNamara in prep.) is revealing that distinctive echinoid biofacies can be recognised on the basis of the ordinal composition of the fauna. Regular and holasteroid echinoids usually comprise a very small component of the

echinoid faunas, which are dominated by spatangoids, cassiduloids and clypeasteroids. The irregular echinoids in particular are unlikely to have suffered much post-mortem transportation, as they are generally found complete, or nearly so. The delicate nature of the spatagoid test means that even minor post-mortem transportation would result in destruction of the test. Two basic biofacies can be recognised: a spatangoid biofacies, usually found in finer-grained sediments, and representing faunas that dwelt in relatively deep, quiet water (e.g. the echinoid fauna of the Rutledge Marl; see McNamara 1991); and a cassiduloid/clypeasteroid biofacies, generally found in coarser-grained calcarenites deposited in a higher hydrodynamic environment, and representing shallow water faunas. Cassiduloids dominated in the early Tertiary (e.g. the Late Eocene Tortachilla and Nanarup Limestone faunas of South and Western Australia respectively) but were partially replaced by clypeasteroids in later Tertiary faunas (e.g. some of the Miocene formations of the Murray Basin). Challis (1979) has recognised a range of generic echinoid biofacies in Miocene strata of the Maltese Islands. She has likewise noted that spatangoid-dominated biofacies correspond more with fine-grained sediments deposited in deeper water than do cassiduloid/clypeasteroid-dominated biofacies, which are characteristic of coarser-grained sediments deposited under shallower-water conditions.

Of the Late Oligocene echinoid faunas of the Torquay Basin, the Point Addis Limestone fauna can be placed within the cassiduloid/clypeasteroid biofacies, while the Waurn Ponds Limestone fauna is characterised as a spatangoid biofacies. Although both of these units are dominated by bryozoal calcarenites, the nature of the echinoid biofacies suggests that the Point Addis Limestone was deposited in shallow water whereas the Waurn Ponds Limestone was deposited under deeper-water conditions. This conclusion is supported by the rarity in the Waurn Ponds Limestone of regular echinoids, which are absent in other deep-water faunas such as those of the Rutledge Marl (McNamara 1991). Unlike the Point Addis Limestone, the Waurn Ponds Limestone bryozoal calcarenites are intercalated with marl and clay horizons. The intermediate nature of the echinoid biofacies of the Jan Juc Formation suggests that it may have been deposited under water depths intermediate between those under which the other two units were deposited.

REFERENCES

ABELE, C., 1976. Central coastal basins. In *Geology of Victoria*, J. G. Douglas & J. A. Ferguson, eds, Geological Society of Australia, Melbourne, 303–322.

CHALLIS, G. R., 1979. Miocene echinoid biofacies of the Maltese Islands. *Annales géologique des pays helléniques, Tome hors série* 1979, fasc. 1: 253–262.

GILL, E. D., 1952. Notes on some spines of a Tertiary echinoid from Victoria. *Proceedings of the Royal Society of Victoria* 64: 1–3.

KRUSE, P. D. & PHILIP, G. M., 1985. Tertiary species of the echinoid genus *Eupatagus* from southern Australia. *Special Publications, South Australian Department of Mines & Energy* 5: 167–185.

McCOY, F., 1882. *Prodromus of the Palaeontology of Victoria; or, Figures and Descriptions of Victorian Organic Remains*, Decade VII, Geological Survey of Victoria, Melbourne, 30 p., pls 61–70.

McNAMARA, K. J., 1985. Taxonomy and evolution of the Cainozoic spatangoid echinoid *Protenaster*. *Palaeontology* 28: 311–330.

McNAMARA, K. J., 1987, Taxonomy, evolution, and functional morphology of southern Australian Tertiary hemiasterid echinoids. *Palaeontology* 30: 319–352.

McNAMARA, K. J., 1990. Echinoids. In *Evolutionary Trends*, K. J. McNamara, ed., Belhaven Press, London, 205–231.

McNAMARA, K. J., 1991. A guide to the echinoids of the Middle Miocene Rutledge Marl, Victoria. *Victorian Naturalist* 108: 8–19.

McNAMARA, K. J. & PHILIP, G. M., 1984. A revision of the spatangoid echinoid *Pericosmus* from the Tertiary of Australia. *Records of the Western Australian Museum* 11: 319–356.

McNAMARA, K. J., PHILIP, G. M. & KRUSE, P. D., 1986. Tertiary brissid echinoids from southern Australia. *Alcheringa* 10: 55–84.

MORTENSEN, T., 1951. *A Monograph of the Echinoidea*, 5 (2), *Spatangoida* II, C. A. Reitzel, Copenhagen, 593 p., 64 pls in separate Atlas.

PHILIP, G. M., 1965. The Tertiary echinoids of southeastern Australia. III. Stirodonta, Aulodonta, and Camarodonta (1). *Proceedings of the Royal Society of Victoria* 78: 181–196.

PHILIP, G. M. & FOSTER, R. J., 1971. Marsupiate Tertiary echinoids from south-eastern Australia and their zoogeographic significance. *Palaeontology* 14: 666–695.

A NEW SPECIES OF *ISCHNOCHITON (CHARTOPLAX)* IREDALE & HULL, 1924 (MOLLUSCA: POLYPLACOPHORA) FROM SOUTH AUSTRALIA, AND THE STATUS OF *ISCHNOCHITON (STENOCHITON) PALLENS* ASHBY, 1900

Tonia G. Cochran

Department of Invertebrate Zoology, Museum of Victoria, 328 Swanston Street, Melbourne, Victoria 3000; and Department of Zoology, University of Melbourne, Parkville, Victoria 3052
Present address: Cloudy Bay Road, Bruny Island, Tasmania 7150

Cochran, T. G., 1993:03:31. A new species of *Ischnochiton (Chartoplax)* Iredale & Hull, 1924 (Mollusca: Polyplacophora) from South Australia, and the status of *Ischnochiton (Stenochiton) pallens* Ashby, 1900. *Proceedings of the Royal Society of Victoria* 105 (1): 49–56. ISSN 0035-9211.

Ischnochiton (Chartoplax) Iredale & Hull, 1924 is redefined, mainly on the basis of characteristic girdle and radular morphology. The new species *I. (Chartoplax) nubilus* is described and compared with the type and only other known species of the subgenus, *I. (C.) purus* Sykes, 1896. *Ischnochiton (Stenochiton) pallens* Ashby, 1900 is a junior subjective synonym of *I. (C.) purus*.

THE ENDEMIC southern Australian polyplacophoran genus *Stenochiton* H. Adams & Angas, 1864, hitherto represented by four species, belongs to the family Ischnochitonidae (Iredale & Hull 1924, 1927; Cotton & Godfrey 1940; Cotton 1964). During a recent study of the Ischnochitonidae from this region, it was recognized that the type specimens of one of the species previously assigned to this genus, *Ischnochiton (Stenochiton) pallens* Ashby, 1900, actually represent two species, both of which belong to *Ischnochiton* Gray, 1847. Both species are here assigned to *Ischnochiton (Chartoplax)* Iredale & Hull, 1924, and one of the species, also represented by additional material from South Australia, is newly named.

All material examined is deposited in the Museum of Victoria, Melbourne (NMV) and the South Australian Museum, Adelaide (SAM). Registration numbers and measurements of all specimens used in this study are on file in the Department of Invertebrate Zoology, NMV. The methodologies for obtaining morphometric and meristic measurements, and scanning electron microscope (SEM) preparations, are described by Cochran (1988). Terminology for morphology of valves follows that of Kaas & Van Belle (1985).

SYSTEMATICS

Family Ischnochitonidae Dall, 1889
Subfamily Ischnochitoninae Dall, 1889

Genus Ischnochiton Gray, 1847
Subgenus Ischnochiton (Chartoplax)
Iredale & Hull, 1924

Haploplax (Chartoplax) Iredale & Hull 1924: 295.

Type species. Ischnochiton (Haploplax) pura [sic] Sykes, 1896.

Diagnosis. Ischnochiton of small size (to 22 mm long), elongate to elongate-ovate, round-backed or carinated with moderately high dorsal elevation. Surface of tegmentum ridged with shallow grooves connecting apical caps of aesthetes; ridges longitudinally-arranged on central and antemucronal areas, radially-arranged on terminal (postmucronal area and anterior valve) and lateral areas of valves; granules and pits may be present. Insertion teeth of intermediate valves with 1–3 slits. Dorsal girdle scales minute (to 60 μm wide), elongated, dorso-ventrally flattened or slightly convex, and striated with narrow ridges which do not extend to distal margin of scales. Ventral girdle scales smooth or striated. Central teeth of radula broad, hardly folded; blade of first lateral teeth laterally curved, broad, not folded; major lateral teeth bicuspidate, cusps almost equal in size, with dorsal hump or angularity; spatulate uncinal teeth with shallow groove or with thickened edge and no groove.

Remarks. Iredale & Hull (1924) proposed *Haploplax (Chartoplax)* for *Ischnochiton (Haploplax) purus*, which they separated from other species of *Haploplax* on the basis of its

Character	I. (Ischnochiton)	I. (Chartoplax)	I. (Haploplax)
Radula			
(a) Denticle cap of major lateral teeth			
(i) size of cusps	approximately equal	approximately equal	inner cusp much longer and larger than outer cusp
(ii) dorsal surface	rounded	angular/humped	rounded
(b) First lateral teeth	blade folded, restricted to apex of teeth	blade not folded, laterally curved	blade folded, enlarged to extend down outer edge of teeth
Dorsal girdle scales			
(a) distal margin	rounded or obtusely pointed	flattened	obtusely pointed
(b) shape	convex	flattened	convex
(c) striae	distinct; extend to margin; grooves and ridges of approximately equal size	distinct; do not extend to margin; ridges thin, grooves wide and deep	indistinct; extend to margin; grooves and ridges of approximately equal size

Table 1. Comparison of selected characters of *I. (Ischnochiton), I. (Chartoplax)* and *I. (Haploplax).*

small, elongate, smooth and flattened girdle scales. More recent authors (eg. Kaas & Van Belle 1980, 1987) have not recognised *Chartoplax* but have assigned *purus* either to *Ischnochiton* or to *Ischnochiton (Haploplax)*. I consider, however, that the girdle and radula of *purus* and the new species *nubilus* differ sufficiently from those of species assigned to *I. (Ischnochiton)* and *I. (Haploplax)* to justify subgeneric distinction (Table 1). I therefore recognize *Chartoplax* as a subgenus of *Ischnochiton* to accommodate these two species.

Ischnochiton (Chartoplax) purus Sykes, 1896

Ischnochiton (Stenochiton) pallens Ashby 1900 (in part): 86–87, pl. 1, fig. 1B–E (non pl. 1, fig. 1).

Remarks. The type material of *Ischnochiton (Stenochiton) pallens* consists of two specimens, SAM D978 (Ashby 1900, pl. 1, fig. 1B–E) and SAM D11728 (Ashby 1900, pl. 1, fig. 1). In his original description Ashby did not designate a holotype, and although he labelled the specimens "type" and "co-type" respectively, this action does not constitute a valid type designation (ICZN Article 72(b)(vii)). The specimens were incorrectly referred to by Zeidler & Gowlett (1986) as the holotype (SAM D978) and paratype (SAM D11728), following Cotton & Godfrey (1940) and Cotton (1964). The citing of SAM D978 as holotype by Cotton & Godfrey (1940) constitutes a valid designation of lectotype (ICZN Article 74(a); also "designation of

lectotype by inference of holotype", ICZN Article 74(b)).

Ashby's illustrations of the lectotype show wide, shallow insertion slits and a jugal notch in the anterior valve, a wide, rounded posterior valve and flattened apophyses, and granulose tegmental sculpture. In these features, and in the rectangular shape of most of the intermediate valves in dorsal view, the specimen resembles *Ischnochiton (Chartoplax) purus*, and *pallens* is here considered to be a junior subjective synonym of that species. The trapezoidal shape of the intermediate valve of the lectotype of *pallens* shown in pl. 1, fig. 1 of Ashby (1900) superficially resembles an intermediate valve of *I. (C.) nubilus* sp. nov., but the figured valve is valve II which is commonly this shape in species of *Ischnochiton*. The posterior valve of the lectotype of *pallens* figured by Ashby has been lost (Zeidler & Gowlett 1986, as holotype).

The paralectotype of *pallens* differs from the lectotype in a number of characters (see below) and is here considered to belong to a separate, hitherto unnamed species. The specimen is selected as the holotype of *I. (C.) nubilus* sp. nov.

In a later discussion of *pallens*, Ashby (1918) referred to "the three original specimens dredged by Dr J. C. Verco", thus implying the existence of a third type specimen. The third specimen to which he was referring (SAM D14491) was, according to the original label, dredged in Spencer Gulf in February 1905, five

years after the publication of the original description of *I. (S.) pallens*. This specimen is thus not considered to have any type status.

When *I. (Stenochiton) pallens* was originally described, the geographic range of *I. (Chartoplax) purus* was not known to extend as far west as South Australia. The intermediate valves of *I. (C.) purus* were also considered to contain one slit (Sykes 1896; Iredale & Hull 1924, 1927), whereas I have found that there are as many as three slits. The presence of two slits in two of the intermediate valves of the lectotype of *I. (S.) pallens* probably led Ashby (1900) to assign his species to *Stenochiton*, because the two representatives of that genus known at the time (*S. longicymba* and *S. pilsbryanus*) have multifissurated intermediate valves. The morphological similarities between *I. (C.) purus* and *I. (C.) nubilus* sp. nov., together with the paucity of information on both species, probably led to their inclusion in *I. (S.) pallens* by Ashby.

Ischnochiton (Chartoplax) nubilus sp. nov.

Figs 1, 2

Ischnochiton (Stenochiton) pallens Ashby 1900 (in part): 86–87, pl. 1, fig. 1 (non pl. 1, fig. 1B–E).—Nierstrasz 1905: 19.—Zeidler & Gowlett 1986: 108.
Ischnochiton pallens.—Iredale 1910: 158.
non *Ischnochiton pallens.*—Torr 1912: 143.—Gatliff & Gabriel 1917: 26–27 [= *Stenochiton cymodocealis* Ashby, 1918].—Ashby 1926: 15, pl. 1, fig 1 [= *Ischnochiton lineolatus* (Blainville, 1825)].
Stenochiton pallens.—Ashby 1918: 75–76, pl. 14, figs 14A, B.—Ashby 1923: 263.—Iredale & Hull 1924: 287–288, pl. 37, fig 8.—Ashby 1927: 116.—Iredale & Hull 1927: 32, pl. 5, fig 8.—Cotton & Godfrey 1940: 511, fig 504.—Cotton 1964: 50, fig 49.—Zeidler & Gowlett 1985: 37.
non *Stenochiton pallens.*—Ashby 1920: 284.—Ashby 1921: 150–151.—Gatliff & Gabriel 1931: 219 [= *S. cymodocealis* Ashby, 1918].

Etymology. The specific name (L. nubilus = cloudy, covered with clouds) refers to the colour pattern on the tegmentum.

Type material. Holotype: SAM D11728 (paralectotype of *Ischnochiton (Stenochiton) pallens*), from Gulf St Vincent, South Australia (SA); dredged by J. C. Verco, ex Ashby collection. Dried, curled specimen measuring approximately 16 × 6 mm. Paratypes: SAM D17592 (1 preserved specimen), Reevesby Island, and SAM D17593 (1 partially disarticulated preserved specimen), Marum Island, northern and northwestern points, both islands in Sir Joseph Banks Group, Spencer Gulf, SA; SAM D15127 (1 dried specimen), Brighton, SA; NMV F54266 (1 preserved specimen), Point Sinclair, SA.

Other material examined. SAM D14491 (1 dried specimen), Spencer Gulf, SA; SAM D17594–D17598 (7 preserved specimens), Marum Island, Spencer Gulf, SA; SAM D14928 (1 dried specimen), Brighton, SA; NMV F52986 (1 dried specimen), off Cape Donington, SA.

Diagnosis. Animal elongated (total length:total width > 2.5:1), round-backed. Surface of tegmentum glossy, finely ridged; insertion teeth adjacent to posterior edge of anterior and intermediate valves triangular in shape; intermediate valves with 1–2 slits; dorsal girdle scales almost rectangular, glossy, striated with 7–12 narrow ridges having wide, deep grooves between them.

Description

General. Specimens to 22 mm long, elongated, with an average total length:total width ratio of 2.59 ± 0.26:1 (mean ± sd), n = 14 (Fig. 1A, B); round-backed (Fig. 1M), with a moderate to high dorsal elevation (height:width ratio of valve V) of 0.40 ± 0.09:1, n = 14.
Tegmentum. Colour fawn or cream, mottled with pale pink, pale brown and mauve; dark red-brown markings also present on some specimens; tegmentum glossy, microscopically sculptured with very fine ridges, with smooth polished appearance under low magnification. Apical caps of megalaesthetes approximately three times size of subsidiary caps (Fig. 2A).
Valves. Anterior valve (Fig. 1C, I) broad, more than twice as wide as long (width:length ratio of valve I = 2.08 ± 0.13:1, n = 14); slope slightly convex, posterior margin widely V-shaped to U-shaped. Intermediate valves (Fig. 1D, J) trapezoid in dorsal view, relatively long (width:length ratio of valve V = 2.23 ± 0.35:1, n = 13); posterior margin straight, lateral areas slightly raised. Posterior valve (Fig. 1E, K) elongated (width:length ratio of valve VIII = 1.09 ± 0.08:1, n = 13), tapering posteriorly; mucro sub-median (ratio of distance between anterior margin and mucro:total length of valve VIII = 0.59 ± 0.04:1, n = 13), pointed and slightly raised; diagonal line straight to slightly concave, forming an equilateral triangle with anterior margin; dorsal surface of antemucronal area typically slightly convex (Fig. 1K) but in some specimens slightly concave adjacent to mucro (Fig. 1K'); postmucronal slope usually convex immediately below mucro and becoming concave near base of valve, but in some specimens totally concave.
Articulamentum. White with red-brown markings in muscle scars; apophyses small, tapering
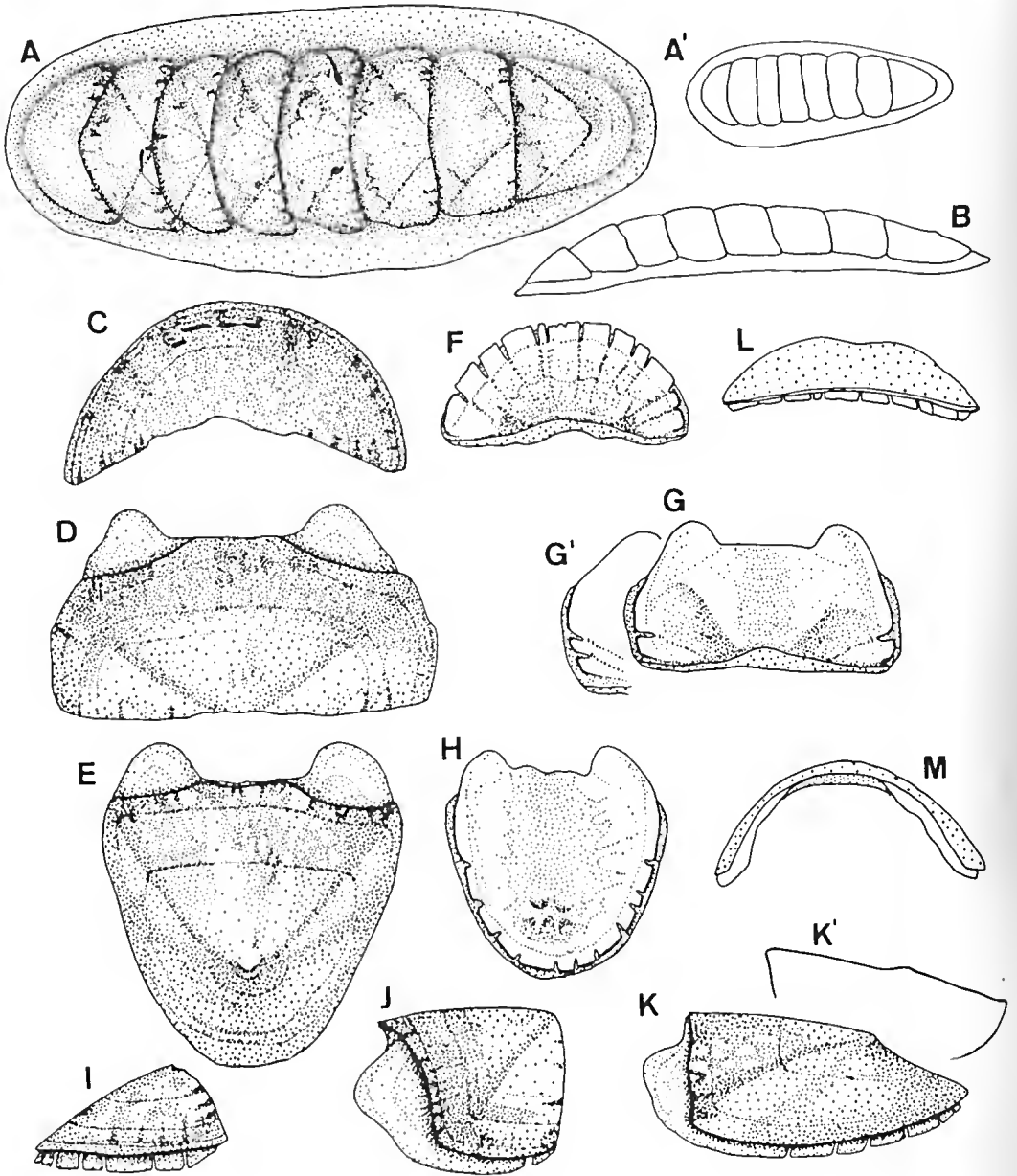
Fig. 1. *Ischnochiton nubilus* sp. nov. A–B, whole specimen. A, dorsal view, × 6.5; A', dorsal view showing posterior tapering, × 2.4; B, lateral view, × 4.7. C–E, dorsal view of valves, × 3.5. C. valve I; D, valve V; E, valve VIII. F–H, ventral view of valves, × 2.5. F, valve I; G, valve V; G', valve VII; H. valve VIII. I–K, lateral view of valves, × 3.5. I, valve I; J, valve V; K, K', valve VIII from two different specimens. L, M, anterior view of valves, × 2.5. L, valve I; M, valve V. A–B, paratype SAM D15127; A', C–M, paratype SAM D17593; K', paratype SAM D17592.
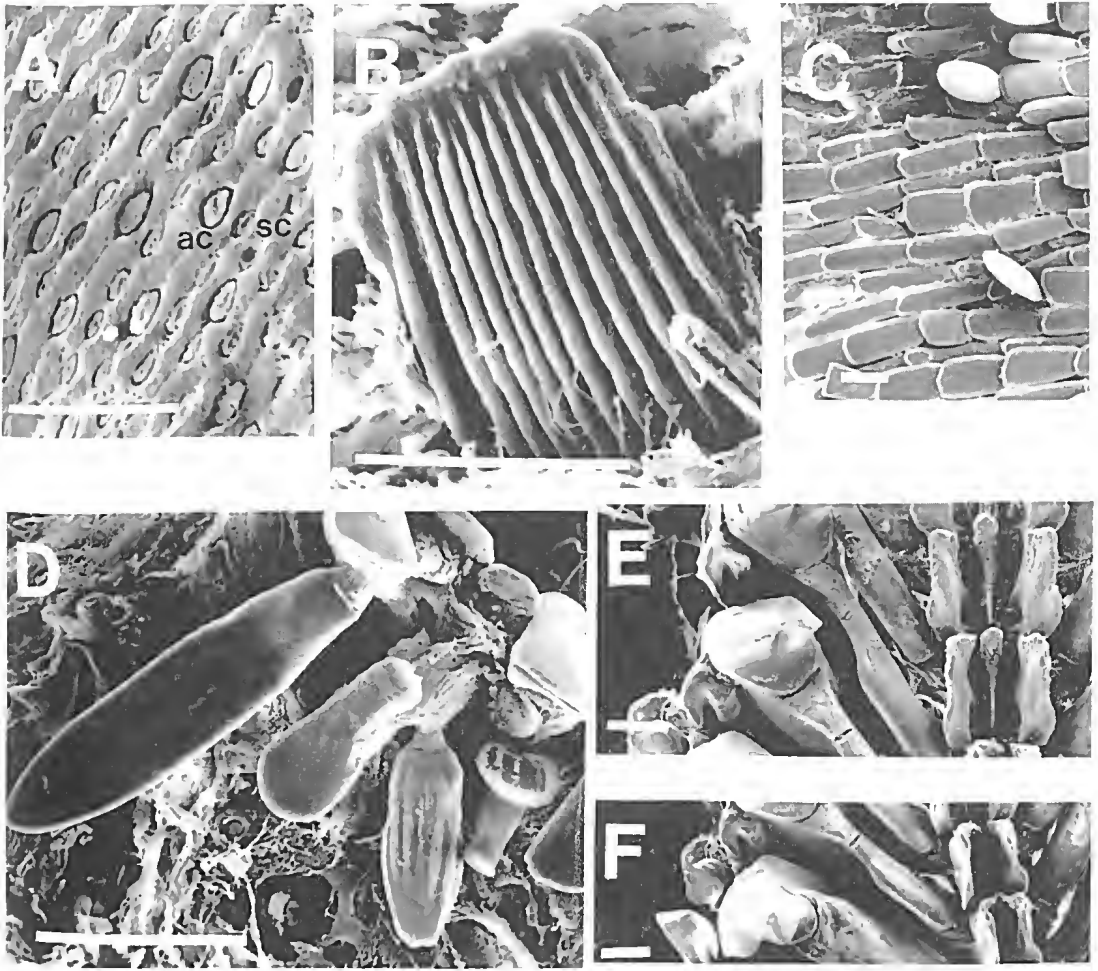
Fig. 2. Ischnochiton nubilus sp. nov., paratype SAM D17593. A, tegmentum showing apical caps (AC) and subsidiary caps (SC) of aesthetes, connected by longitudinal grooves. B, dorsal girdle scale. C, ventral girdle scales. D, marginal scales. E, F, radula. Scale bars: A, C–F = 50 μm; B = 25 μm).

with an outer lateral flange (Fig. 1D); apophyses connected across jugal sinus by a narrow shelf in posterior valve (Fig. 1E); jugal sinus wide, more than one-third width of valve (ratio of jugal sinus:apophysis width = 0.43 ± 0.12:1, n = 4)(Fig. 1D, G); insertion teeth project beyond edge of tegmentum in anterior valve (Fig. 1F, I); teeth adjacent to posterior margin of anterior and intermediate valves tapered posteriorly, triangular (Fig. 1I, J); slits narrow, longer in anterior and intermediate valves (400 μm long × 40 μm wide) than in posterior valve (200 × 40 μm) (Fig. 1F–H, L); slit formula 9-13/1-2/9-12; valves II–V with one slit; valve VII with two slits

(Fig. 1G′); valve VI with typically one slit, but two in some specimens.

Girdle. Width of girdle 14.94 ± 3.02% (n = 10) of total width of spirit-preserved specimens, in some specimens wider anteriorly, giving animal a posteriorly-tapered appearance (Fig. 1A′); girdle white, or fawn with red-brown markings. Dorsal scales minute (20–50 μm wide), rectangular, with a tendency to stand upright on girdle; scales of uniform size throughout girdle, glossy, microscopically striated with 7–12 deep grooves (Fig. 2B); ventral scales glossy, oval to rectangular, dorso-ventrally flattened, blunt-ended, 50–75 × 20–30 μm in size (Fig. 2C); mar-

ginal spicules straight, pointed, 100×25 μm in size, interspersed with blunt-tipped, irregularly-shaped scales striated with 4–5 longitudinal ridges (Fig. 2D).

Gills. 19–25 pairs of long, narrow ctenidia extending from level of posterior margin of valve III; nephridiopore and gonopore separated by two ctenidia, situated typically between gills 6–7 and 8–9 respectively.

Radula (Fig. 2E, F). Central tooth narrow, elongated, apically broader and rounded; first lateral teeth broad, flattened, blade laterally curved, not folded, oriented parallel to central tooth, inner surface concave at base; major lateral teeth with obtusely-pointed, bidentate cusps, with dorsal angularity; spatulate uncinal teeth with shallow dorsal groove.

Distribution and habitat. From Point Sinclair (32°06'S, 132°58'E) to Gulf St Vincent (34°10'–35°10'S, 137°45'–138°30'E) in South Australia. Records of *I. (C.) nubilus* (as *I. (Stenochiton) pallens*) from Port Phillip Bay, Victoria (Gatliff & Gabriel 1917, 1931; Ashby 1918) are based on the misidentification of a single, badly damaged specimen of *Stenochiton cymodocealis* Ashby 1918 (NMV F54480); the girdle scales are smooth, apically-rounded and characteristic of the latter species (Fig. 3B). The dorsal girdle scales of *I. (C.) nubilus* are rectangular and striated (Fig. 2B).

Ischnochiton (Chartoplax) nubilis lives on pebbles in sand, or amongst rubble or the sea-grass *Posidonia* (Zeidler & Gowlett 1985), at depths of up to 18 m.

Remarks. Although the new species superficially resembles members of *Stenochiton*, it is placed in *Ischnochiton* on the basis of the morphology of valves, girdle scales and radula. The finely-ridged tegmental sculpture, the morphology of the aesthetes (Fig. 2A) and the striated dorsal girdle scales (Fig. 2B) are characteristic of *Ischnochiton*. The tegmentum and dorsal girdle scales of *Stenochiton* are smooth (Fig. 3A, B). *I. (C.) nubilis* can be readily separated from species of *Stenoplax* Dall, 1879 by the bicuspidate denticle cap of the radula (Figs 2E, F); in *Stenoplax* this structure is tricuspidate (Bullock 1985).

I. (C.) nubilus shares several morphological characters with *I. purus*, with which it is sympatric in South Australia. The two species may be distinguished by the features listed in Table 2.

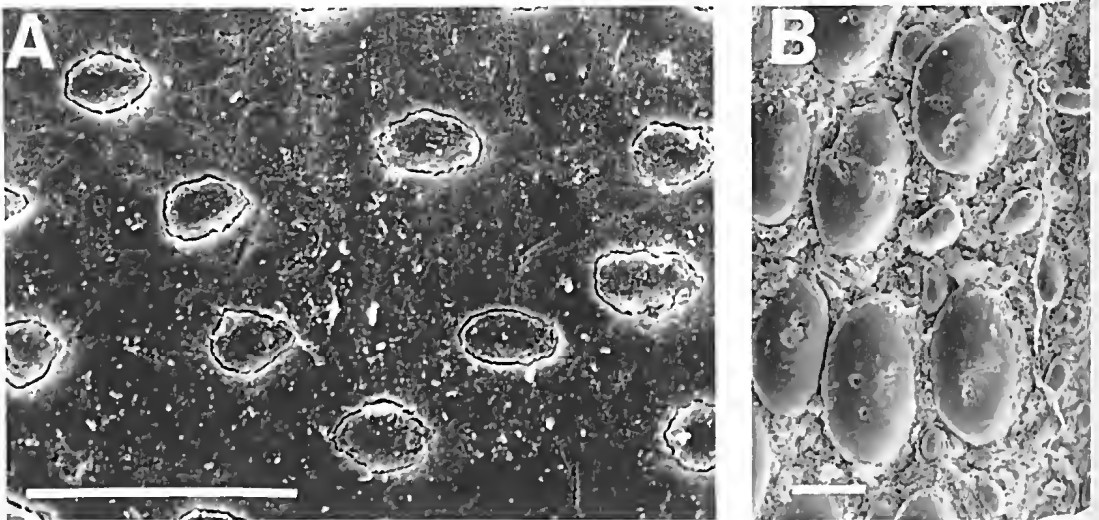*Fig. 3. Stenochiton cymodocealis* Ashby, NMV F51423. A, tegmentum showing aesthete caps. B, dorsal girdle scales. Scale bars = 50 μm).

Character	I. (C.) nubilus	I. (C.) purus
Colour of tegmentum	cream/fawn mottled with pink, pale brown and mauve	white/cream
Tegmental sculpture	granules/pits absent	granules/pits present
Shape of valves III–VII (dorsal view)	trapezoid	rectangular
Shape of intermediate valves (anterior view)	round-backed	carinated
Morphology/size of insertion slits (anterior valve)	long, narrow 400 × 40 µm	wide, U-shaped 360 × 120 µm
Edge of insertion teeth	straight, sharp	crenulated
Shape of insertion teeth adjacent to posterior margin of anterior and intermediate valves	tapered posteriorly (triangular)	not tapered (rectangular)
Number of striae on dorsal girdle scales	7–12	12–16
Ventral girdle scales	smooth	striated
Typical positions of nephridiophore and gonopore, respectively	6 & 7/8 & 9 (separated by two ctenidia)	5 & 6/6 & 7 (separated by one ctenidium)

Table 2. Comparison of selected characters of *Ischnochiton (Chartoplax) nubilus* sp. nov. and *I. (C.) purus.*

REFERENCES

ASHBY, E., 1900. Definitions of two new species of South Australian Polyplacophora. *Transactions of the Royal Society of South Australia* 24: 86–88.

ASHBY, E., 1918. Monograph on the genus *Stenochiton* (Order Polyplacophora), with descriptions of two new species. *Transactions of the Royal Society of South Australia* 42: 65–78, pls 13, 14.

ASHBY, E., 1920. Further notes on Australian Polyplacophora, with additions and corrections of the 1918 distribution list. *Transactions of the Royal Society of South Australia* 44: 283–292.

ASHBY, E., 1921. Description of Bracebridge Wilson collection of Victorian chitons, with description of two new species. *Proceedings of the Royal Society of Victoria* 33: 149–159, pl. 8.

ASHBY, E., 1923. Notes on the genus *Stenochiton* and the discovery and recognition of the type of Blainville's *Chiton longicymba* in *Stenochiton juloides*, Adams & Angas. *Proceedings of the Malacological Society of London* 15: 260–265.

ASHBY, E., 1926. Victorian chitons. *Victorian Naturalist* 43: 7–16.

ASHBY, E., 1927. Notes on, and additions to, the chiton fauna of north-west Tasmania, together with a brief review of the genus *Stenochiton. Papers and Proceedings of the Royal Society of Tasmania* (1926): 92–117.

BULLOCK, R. C., 1985. The *Stenoplax limaciformis* (Sowerby, 1832) species complex in the New World (Mollusca: Polyplacophora: Ischnochitonidae). *The Veliger* 27: 291–307.

COCHRAN, T. G., 1988. A new species of *Ischnochiton* (Mollusca: Polyplacophora: Ischnochitonidae) from South Australia, with a discussion of the status of *Ischnochiton levis* Torr, 1912. *Proceedings of the Royal Society of Victoria* 100: 1–7.

COTTON, B. C., 1964. *South Australian Mollusca: Chitons.* Government Printer, Adelaide, 151 p.

COTTON, B. C., & GODFREY, F. K., 1940. *The Molluscs of South Australia, Part 2. Scaphopoda, Cephalopoda, Aplacophora and Crepipoda.* Government Printer, Adelaide, 469–590.

GATLIFF, J. H. & GABRIEL, C. J., 1917. Additions to and alterations in the catalogue of the marine shells of Victoria. *Proceedings of the Royal Society of Victoria* 30: 21–31, pl. 3.

GATLIFF, J. H. & GABRIEL, C. J., 1931. Additions to and alterations in the catalogue of Victorian marine mollusca. *Proceedings of the Royal Society of Victoria* 43: 202–232.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE, 1985. *International Code of Zoological Nomenclature*, 3rd edn. International Trust for Zoological Nomenclature, London, 338 p.

IREDALE, T., 1910. Notes on Polyplacophora, chiefly Australasian (Part 2). *Proceedings of the Malacological Society of London* 9: 153–162.

IREDALE, T & HULL, A. F. B., 1924. A monograph of

the Australian loricates (Phylum Mollusca—Order Loricata) 3. *Australian Zoologist* 3: 277–297, pls 35–37.

IREDALE, T. & HULL, A. F. B., 1927. *A Monograph of the Australian Loricates (Phylum Mollusca—Order Loricata).* Royal Zoological Society of New South Wales, Sydney, 168 p., 21 pls.

KAAS, P. & VAN BELLE, R. A., 1980. *Catalogue of Living Chitons.* Dr W. Backhuys, Rotterdam, 144 p.

KAAS, P. & VAN BELLE, R. A., 1985. *Monograph of Living Chitons (Mollusca: Polyplacophora). O. Neoloricata: Lepidopleurina,* vol. I, E. J. Brill/ Dr W. Backhuys, Leiden, 240 p.

KAAS, P. & VAN BELLE, R. A., 1987. *Catalogue of Living Chitons (Mollusca: Polyplacophora). Suborder Ischnochitonina: Ischnochitonidae: Chaetopleurinae, Ischnochitoninae* (pars). *Additions to Vols 1 and 2.* E. J. Brill/Dr W.

Backhuys, Leiden, 302 p.

NIERSTRASZ, H. F., 1905. Die Chitonen der Siboga-Expedition. *Siboga Expeditie* 48: 1–112, pls 1–8.

SYKES, E. R., 1896. Report on a collection of Polyplacophora from Port Phillip, Victoria. *Proceedings of the Malacological Society of London* 2: 84–93, pl.6.

TORR, W. G., 1912. South Australian Polyplacophora. *Transactions of the Royal Society of South Australia* 36: 140–170, pls 5–7.

ZEIDLER, W. & GOWLETT, K. L., 1985. Some new and noteworthy records of marine Mollusca from the Sir Joseph Banks Islands, Spencer Gulf, SA. *South Australian Naturalist* 59: 36–38.

ZEIDLER, W. & GOWLETT, K. L., 1986. Mollusc type-specimens in the South Australian Museum. 3. Polyplacophora. *Records of the South Australian Museum* 19: 97–115.

EFFECTS OF STOCK GRAZING ON THE PLANTS OF SEMI-ARID WOODLANDS AND GRASSLANDS

DAVID C. CHEAL

School of Botany, University of Melbourne, Parkville, Victoria 3052

Plant species frequencies from 63 quadrats in semi-arid woodland and grassland in north-western Victoria were used to determine the effects of stock-grazing. It was found that grazing by domestic stock reduced the total species diversity and the native species diversity in these habitats. In addition, grazing adversely affected many native plant species, particularly the perennial component and notably the chenopods, leading to local extinctions. Introduced annuals were decidedly more common in grazed areas. The effects on the long-lived woody dominants were more insidious. There was almost total lack of regeneration of trees and shrubs throughout the grazed areas, and their extinction is inevitable if stock-grazing is maintained.

NEARLY thirty years ago, Hall et al. (1964) reported that for over thirty-five years there had been scant or no regeneration of most of the shrub and tree species on unprotected rangeland in arid South Australia. Since then, similar results have been reported from a variety of sites in arid and semi-arid Australia (e.g. Chesterfield & Parsons 1985, Crisp 1978, Lange & Graham 1983, Lange & Purdie 1976). In other parts of Australia, however, there appears to have been an increase in the density of shrubs in rangeland, in spite of continued stock grazing (Downing 1986, Hodgkinson & Harrington 1985).

In all these studies it has been particularly difficult to separate the effects of the various grazing mammals, principally domestic stock, rabbits and kangaroos. Their different dietary preferences (Downing 1986, Storr 1968, Wilson et al. 1976), along with the stocking rates or population levels, largely determine the impacts of each animal species on the vegetation.

A recent survey of the vegetation communities of north-western Victoria entailed the collection of site-specific floristic data (Land Conservation Council 1987). Many of the study sites were within areas licensed for grazing by domestic stock (principally cattle and sheep). Comparison of these data with data from similar vegetation not included within grazing licences allowed examination of the effects of stock grazing, as distinct from grazing by rabbits or native herbivores (which were present at all sites).

Site descriptions

All sites were from Belah Woodland, Gypseous-plains Grassland, Pine-Buloke Woodland or Sand-plain Grassland, as described in the Mallee Study Area Review (Land Conservation Council 1987). Mean annual rainfall varied from approximately 250 mm in the far north-west to approximately 300 mm in the south-west.

Vascular plant nomenclature follows Ross (1990), unless indicated otherwise.

Belah Woodland was dominated by *Casuarina pauper* with a well-developed and diverse shrubby understorey (in an ungrazed condition) and a well-developed low shrub layer, which included many chenopods. Less-disrupted stands supported many native herbs, both perennial and annual.

Pine-Buloke Woodland was variously co-dominated by *Callitris preissii* and *Casuarina luehmannii* (*sensu* Willis 1972) with an open understorey, usually including *Acacia osswaldii, Pittosporum phillyreoides* and *Santalum acuminatum*. The variably dense field layer was formerly dominated by a variety of native perennial tussock grasses and herbs (Land Conservation Council 1987), which had been replaced by a suite of introduced Mediterranean annuals.

Sand-plain Grassland was a rare vegetation community dominated by *Stipa* and *Aristida*

tussocks, with a variety of native herbs in the inter-tussock spaces. Woody plants were absent. Mediterranean annuals dominated heavily disturbed stands, while native composites (*Helipterum* and *Podolepis* spp.) were common in moderately disturbed stands.

Gypseous-plains Grassland was restricted to the north-west of the study area, where powdery gypsum ("copi") was a distinctive component of the loamy soils. Shrubby chenopods were scattered throughout, the only trees present being rare veteran individuals of *Myoporum platycarpum*. Short-lived annuals, both native and introduced, dominated the field layer.

None of the sites had been recently burnt or showed any evidence of wildfire.

METHODS

The data were collected as part of a regional study of the vegetation communities, as described by Cheal & Parkes (1989). Grossly disturbed areas, such as near watering points, fence lines or tracks, were not sampled. All sampling was conducted from August to November and most quadrats were surveyed in 1986. Quadrats were located in apparently homogeneous vegetation and were consistently 30 m square. All vascular plants growing in or projecting over the quadrat were recorded and assigned a cover-abundance value (see Bridgewater 1981). The proportion of species that could not be identified rarely exceeded 3% in each quadrat.

The complete data set from the Mallee Region of Victoria was scrutinised and all quadrats from non-riverine woodland and grassland were identified and separated for subsequent analysis of grazing impacts.

It was doubtful whether legitimate comparisons of grazed and ungrazed sites could be made for the Big Desert block. Many woodland quadrats in this region had been subject to stock grazing until the extension of Wyperfeld National Park, following the recommendations of the Land Conservation Council in 1977. Other woodland areas had been included within Wyperfeld National Park for many decades. Unfortunately there were few non-riverine woodland quadrats from areas subject to continued licensed grazing. There are notable climatic and soil differences between the Big Desert and Sunset blocks, and it was not considered appropriate to lump data from such disparate areas for comparisons based on inclusion within areas licensed for grazing, particularly when the data set

from areas in the Big Desert subject to on-going grazing was so scanty.

Similarly, quadrats from Hattah–Kulkyne National Park were not included within the analysis. Hattah–Kulkyne has been subject to intense grazing from both sheep and cattle for many decades before declaration and extension of the park. In recent years, domestic stock have been removed but the grazing by rabbits and kangaroos (principally *Macropus fuliginosus*) has been reduced by intense management in some parts of the park and essentially unaffected in other parts. Hattah–Kulkyne supports extraordinarily high densities of kangaroos (Cheal 1986, Coulson 1988). Comparisons of stock-free woodland from Hattah–Kulkyne with woodland nearby, but not subject to this heavy grazing from kangaroos, would only have confused investigation of the effects of grazing by stock. Hence, only quadrats from the Sunset Country (that area of public land bounded by the South Australian border, the Ouyen–Pinnaroo road, the Calder Highway and the Murray River) were included in the analysis.

Maps of the existing grazing licences were scanned and the data set was divided into two, on the basis of whether each quadrat was within an area licensed for stock grazing or not. Thirty-three quadrats were identified from within grazing licences and thirty from areas not so licensed. It is important to emphasise that this distinction did not separate the quadrats into homogeneous subsets—"grazed" and "ungrazed". Areas subject to stock grazing are not subject to uniform impact. Pasture adjacent to watering points and pasture from fertile soils are subject to much heavier grazing (and the consequent physical damage) than the mean for the whole of that licensed area (Foran et al. 1982, Squires & Low 1987). Nevertheless, it was assumed that presence within a licensed area meant that the vegetation was subject to grazing by domestic stock. This somewhat simplistic assumption notably underestimates the impacts of domestic stock, as grazing licences are not subject to uniform disturbance from stock.

The only quadrats from managed nature reserves were a small number from the Pink Lakes State Park. At the date of sampling, licensed grazing by sheep still occurred in the southern half of this park; quadrats from this latter area were thus included within the data set "subject to grazing".

Shannon Diversity Indexes (*sensu* Magurran 1988) were calculated for all quadrats from the licensed and the unlicensed areas, and for the

respective native plant species and introduced plant species communities. Evenness measures were also calculated (though not statistically compared). The diversities were compared using t-tests (Magurran 1988). The effects on individual species of their inclusion within grazing licences were compared using 2 × 2 contingency tables (including Yates' Correction).

RESULTS

One hundred and fifty-three (153) species of vascular plants were recorded from the grazed (= licensed) quadrat data set and 217 species from the ungrazed (= unlicensed) quadrat data set. However, most of these species occurred too infrequently for statistical analysis, which was restricted to the 53 most common and widespread species.

It is inferred that stock grazing significantly decreased the total plant species diversity and the native plant species diversity (Table 1). There was no significant impact of stock grazing on the species diversity of introduced plants.

Tables 2 to 4 compare the impacts of stock grazing on individual plant species. Clearly, in-

		Grazed	Ungrazed	P
All species	Diversity	4.51	5.02	<0.001
	Evenness	0.896	0.933	
Native species	Diversity	4.26	4.74	<0.001
	Evenness	0.902	0.912	
Introduced species	Diversity	3.19	3.14	n.s.
	Evenness	0.866	0.885	

Table 1. Species diversity comparisons.

troduced annuals (including those declared "noxious") were favoured by stock grazing, or seemed unaffected. By contrast, many native plant species, particularly perennial herbs, sub-shrubs and shrubs, were adversely affected by grazing, and were often subject to local elimination. The non-spinescent chenopods were notably affected. It is interesting that two species of very similar growth form were affected in opposite ways: the perennial tussock grass *Stipa eremophila* was adversely affected by grazing, whilst the (more or less) perennial tussock grass *Stipa scabra* subsp. *falcata* was favoured by grazing.

Table 5 presents data on the abundances of rare or threatened plant species (after Gullan et al. 1990), including some of the woody dominants.

DISCUSSION

In spite of the long history of research into the effects of grazing on rangeland flora, arguments about the impacts of grazing by domestic stock on the vegetation in north-western Victoria have been intense and prolonged (Land Conservation Council 1987, 1989). The differential effects of stock, rabbits and native herbivores (principally kangaroos) have proved particularly difficult to determine.

It is clear from the results presented in this paper that rangeland grazing by domestic stock in Victorian semi-arid woodlands and grass-lands eliminates many (principally native) species of plants and favours the establishment and spread of a number of introduced species (principally Mediterranean annuals). The species favoured by grazing are not necessarily

		Frequencies	
		Grazed	Ungrazed
Brassica tournefortii	(annual crucifer)	93	55
Carrichtera annua	(annual crucifer)	20	0
Critesion murinum subsp. *glaucum*	(annual grass)	77	24
Echium plantagineum	(annual dicot herb)	20	0
Erodium cicutarium	(annual dicot herb)	47	15
Onopordum acaulon	(annual composite thistle)	33	0
Reichardia tingitana	(annual composite)	63	30
Shismus barbatus	(annual grass)	57	9
Sisymbrium erysimoides	(annual crucifer)	40	9
Stipa scabra subsp. *falcata*	(short-lived perennial grass)	87	42

Table 2. Species more common in grazed areas. P < 0.05; * = introduced species.

		Frequencies	
		Grazed	Ungrazed
Acacia osswaldii	(perennial shrub)	0	21
Chenopodium desertorum	(perennial chenopod subshrub	0	24
Chenopodium curvispicatum	(perennial chenopod subshrub	7	33
Dodonaea viscosa subsp. *angustissima*	(perennial shrub)	13	39
Einadia nutans	(short-lived perennial chenopod)	7	42
Enchylaena tomentosa	(perennial chenopod shrub)	23	58
Eriochiton sclerolaenoides	(short-lived perennial chenopod)	13	42
*Gynandriris setifolia	(cormous irid)	0	33
Helipterum pygmaeum	(annual composite)	37	67
Helipterum stuartianum	(annual composite)	0	45
Minuria leptophylla	(perennial composite subshrub)	0	21
Pimelea microcephala	(perennial shrub)	0	21
Podolepis canescens	(perennial composite herb)	0	36
Scaevola spinescens	(perennial shrub)	0	18
Sclerolaena diacantha	(short-lived perennial chenopod)	27	88
Stipa elegantissima	(perennial grass)	0	30
Stipa eremophila	(perennial grass)	0	64
Vittadinia condyloides	(short-lived perennial composite)	0	48
Vittadinia gracilis	(short-lived perennial composite)	3	42

Table 3. Species more common in areas without stock grazing. $P < 0.05$; * = introduced species.

Actinobole uliginosum	(annual composite)
Alectryon oleifolius	(woody tree)
Brachyscome lineariloba	(annual composite)
*Bromus rubens	*(annual grass)*
Calandrinia eremaea	(annual dicot herb)
Calotis hispidula	(annual composite)
*Carthamus lanatus	(annual composite thistle)
Crassula colorata	(annual dicot herb)
Crassula sieberiana	(annual dicot herb)
Danthonia caespitosa	(short-lived perennial grass)
Daucus glochidiatus	(annual dicot herb)
Eremophila oppositifolia	(woody shrub)
Erodium crinitum (L)	(annual dicot herb)
Exocarpos aphyllus	(woody shrub)
Goodenia pusilliflora (U)	(short-lived perennial herb)
*Hypochoeris glabra	(annual composite herb)
Isoetopsis graminifolia	(annual composite herb)
*Medicago minima	(annual legume herb)
*Mesembryanthemum crystallinum	(annual dicot herb)
Sclerolaena obliquicuspis	(perennial chenopod shrub)
*Sonchus oleraceus	(annual composite thistle)
Velleia paradoxa (U)	(short-lived perennial dicot herb)
Zygophyllum ammophilum (L)	(annual dicot herb)
Zygophyllum crenatum	(short-lived perennial dicot herb)

Table 4. Species showing no demonstrated effect of stock grazing. $P > 0.05$; * = introduced species; U = significant at $P < 0.1$ and more common in unlicensed areas; L = significant at $P < 0.1$ and more common in licensed areas.

Species		Ungrazed	Grazed
Acacia osswaldii	d	21	0
Alectryon oleifolius	d	39	37
Amyema linophyllum	v	3	3
Callitris glaucophylla	d	0	3
Casuarina luehmannii	d	12	3
Eremophila oppositifolia	v	12	0
Frankenia crispa	r	3	0
Hakea leucoptera	d	0	3
Hakea tephrosperma	d	6	3
Helipterum polygalifolium	r	3	0
Ixiolaena tomentosa	e	3	0
Leptorhynchos waitzia	v	12	0
Maireana lobiflora	v	9	0
Maireana triptera	r	3	0
Phlegmatospermum eremaeum	v	3	0
Pimelea simplex	r	3	0
Podolepis canescens	r	36	0
Rhyncharrhena linearis	v	3	0
Santalum acuminatum	d	6	0
Scaevola spinescens	d	18	0
Senecio platylepis	r	3	0
Templetonia egena	d	12	0
Velleia arguta	r	3	0
Vittadinia condyloides	r	49	0
Vittadinia megacephala	v	3	0
Zygophyllum crenatum	r	18	13
		(24 spp.)	(7 spp.)

Table 5. Frequency of rare or threatened species. e = "endangered in Victoria", v = "vulnerable in Victoria", d = "depleted in Victoria", r = "rare in Victoria", *sensu* Gullan et al. 1990; **bold** = woody tree or shrub usually reaching over 1 m in height.

unpalatable. Wilson (1979) listed *Stipa variabilis* (= *S. falcata*) as "eaten when green" and included the species in his palatability class "A to B", and yet in north-western Victoria *S. falcata* was notably more common in grazed areas than in ungrazed areas (frequencies of 87% v. 42%). Similarly, some highly palatable annuals (e.g. *Hypochoeris glabra, Sonchus oleraceus*; Williams 1969) were neither significantly advantaged nor disadvantaged by stock grazing. Nevertheless, many of the annuals more common under grazing are unpalatable and are thus avoided (e.g. *Brassica tournefortii, Carrichtera annua, Onopordum acaulon*), or are vigorous and short-lived and thus "saturate" the pasture, enabling many plants to flower and set seed before being grazed (e.g. *Critesion murinum, Erodium cicutarium, Schismus barbatus*). Similar conclusions were reached by Holzappel et al. (1992) on the effects of human-caused disturb-

ance (principally rangeland grazing) along an environmental gradient in Israel. Their study demonstrated that disturbance led to an overall decrease in plant species diversity, with local endemics giving way to Mediterranean elements, principally annuals. Such changes in plant species composition after consistent disturbance appear to be a distinctive feature of Mediterranean climates (Grubb & Hopkins 1986).

Most of the species that decreased in frequency when grazed were long-lived native perennials. The shrubby chenopods were particularly disadvantaged. Only *Sclerolaena obliquicuspis* remained common in grazed areas, as was also reported by Mitchell & Wilcox (1988) who described the species as ". . . unattractive to stock . . . eaten only as seedlings or in poor seasons . . . appears to increase under heavy grazing at the expense of more palatable bindiis" (p. 64). In north-western Victoria not only were the palatable chenopods (see Mitchell & Wilcox 1988) adversely affected by grazing (e.g. *Chenopodium curvispicatum, Eriochiton sclerolaenoides, Sclerolaena diacantha*) but also those that are normally considered less palatable (e.g. *Enchylaena tomentosa*). Wilson (1979) described this last species as ". . . only eaten in drought" and ". . . its absence an indicator of heavy grazing". Species absence in grazed areas may have been a direct effect of grazing by domestic stock or a more indirect outcome, e.g. the loss of the woody tree and shrub strata thus removing shelter for germinating seedlings or perches from which animals drop seed from fleshy fruit (see Fig. 1).

It is striking that *Dodonaea viscosa* subsp. *angustissima* was adversely affected by grazing. This tall shrub is one of those species reported to have become common in rangelands of western New South Wales and is there considered a "woody weed" (Hodgkinson & Harrington 1985). Nevertheless, as Downing (1986) also pointed out, using the example of *Dodonaea* spp., after removal of the palatable vegetation by grazing, stock switch to less palatable species that were previously avoided.

Species other than the long-lived chenopods were also adversely affected by grazing. The annual composites *Helipterum pygmaeum* and *Helipterum stuartianum* were surprisingly less common with grazing; Cunningham et al. (1981: 692) recorded the latter as ". . . largely ignored by stock except in times of drought". The perennial composites were also greatly reduced by grazing, including species elsewhere described

as not particularly palatable to stock (Cunningham et al. 1981), e.g. *Podolepis canescens* and *Vittadinia* spp.

It is apparent that licensed grazing of public land as practised in north-western Victoria (i.e. annual grazing licences consistently returned to the former licensees and usually without any rangeland assessment on renewal) led to extensive weed invasion and establishment, replacement of native perennial species by introduced annuals, and elimination of rare and threatened species and of the woody dominants, thus converting woodlands into annual pastures.

From 1845 onwards, pastoral settlement spread throughout all the suitable rangeland in north-western Victoria (plus a substantial proportion of the land that subsequently proved to be unsuitable for rangeland grazing). By 1871, 425,000 sheep were being grazed on over 3,000,000 ha of rangeland (Land Conservation Council 1987). Grazing by domestic stock has been a consistent use since that date and much of the former woodland is now represented by isolated veteran individuals of the more long-lived trees over a strongly seasonal pasture dominated by introduced annuals. Those quadrats identified in this study as "unlicensed" (and hence "ungrazed") were nevertheless formerly grazed, some as recently as 1981–82. The differences in

vegetation composition are a measure of both the heavy grazing of former years (persistent in the quadrats identified as "licensed") and the rapidity of response of the flora to release from stock grazing. It is notable that up to half of the quadrats in unlicensed areas had been recently part of grazing licences (within the last 5 years or so), and presumably supported a flora indistinguishable from that of the "licensed" set. Although the plant species composition at the various sites was assessed over only two seasons, and sites were not monitored upon release from grazing by domestic stock, long-term effects were inferred from the comparisons. There were clear differences in plant species composition between the grazed and the ungrazed quadrats. It is likely that, as the shorter-lived perennials increased rapidly in abundance, there was a consequent decrease in the formerly dominant introduced annuals.

However, the pattern for the long-lived woody dominants was quite different. Recent regeneration (i.e. within the last few decades), either by seed or by resprouts (suckers), was observed only rarely for all of the taller woody species. On the few occasions when such regeneration was observed it was restricted to isolated reserves, surrounded by private cropland, e.g. Yarrara Flora and Fauna Reserve (predominantly Belah

Fig. 1. The effects of stock-grazing may be indirect; *Enchylaena tomentosa* and *Rhagodia spinescens* preferentially establish in the shelter provided by canopies of (in this case) *Alectryon oleifolius*.

Fig. 2. *Alectryon oleifolius*, shores of Lake Beeking; note the prominent browse-line and the lack of regeneration.

Woodland). Regeneration of the formerly dominant trees and shrubs, notably *Acacia osswaldii, Casuarina luehmannii, Exocarpos aphyllus, Hakea leucoptera, Hakea tephrosperma, Santalum acuminatum, Templetonia egena* and *Myoporum platycarpum* subsp. *platycarpum*, was extremely rare (although seed regeneration of *M. platycarpum* subsp. *perbellum, sensu* Chinnock 1992, was common in adjoining mallee shrublands after fire). Nevertheless, for most of these trees and tall shrubs of woodlands the data did not demonstrate any adverse effects due to grazing. Most of the tall woody dominants held at least part of their foliage beyond the reach of both sheep and cattle (see Fig. 2). Although there may have been no regeneration, these are all long-lived species and veteran (though senescent) individuals remain scattered through the landscape. In addition, many quadrats that lacked these species would probably have supported them prior to settlement and the resultant disturbance. Almost the only rare or threatened species to persist in licensed areas were those woody dominants that grew taller than stock could reach.

It is suggested that regeneration of these species is strongly episodic, requiring an unusual succession of climatic events. Chesterfield & Parsons (1985) reported that mammal grazing was important in strongly limiting regeneration of the three tree species that they investigated, i.e. *Alectryon oleifolius, Casuarina pauper* and *Myoporum platycarpum*. The former two species had failed to regenerate for many decades and populations were continuing to decline to such an extent that severe decline or extinction was predicted for *A. oleifolius*. Lange & Purdie (1976) were similarly pessimistic about the survival prospects of *Acacia sowdenii* in grazed landscapes, as was Crisp (1978) for *Acacia aneura* and Hall et al. (1964) for a variety of woody species at Koonamore. In all these situations, seedling regeneration and establishment is strongly tied to unusual climatic events, principally at least two successive seasons of extended summer rainfall and mild weather (Chesterfield & Parsons 1985, Gardiner 1986, Hodgkinson & Harrington 1985). These events are rare; Hodgkinson & Harrington (1985) recorded only four establishment episodes in western New South Wales between the late nineteenth century and the early 1980s. The coincidence of heavy grazing and these critical episodes will have dramatic effects on the persistence of the woody dominants of non-riverine woodlands. Removal of this grazing pressure is a necessary pre-requisite for re-establishment of the woody dominants (see Fig. 3), but the response may be considerably delayed. It may be twenty years or more before any of these woody species regenerates in any abundance, and regeneration will be prevented if the remnant veterans continue to decline, thus eliminating the only *in situ* seed sources.

Fig. 3. Regeneration in the absence of grazing; *Casuarina luehmannii* on a roadside.

The data presented in this paper distinguish the effects of rangeland grazing by domestic stock from the impacts due to rabbits, other feral herbivores and native herbivores, at the particular population levels that applied in north-western Victoria at the time of the study. Dietary preferences alter with availability of preferred forage. Shortage of preferred species (whether due to drought or high population levels of competitors) inevitably lead to increasingly unpalatable species being exploited (Downing 1986, Mitchell & Wilcox 1988, Wilson 1979). Nevertheless, given the tenuous nature of regeneration of the critical dominants characteristic of the woodlands of north-western Victoria, it would be very difficult, and probably impossible, to derive and administer stocking rates that would also permit maintenance of these woodlands.

ACKNOWLEDGEMENTS

REFERENCES

BRIDGEWATER, P., 1981. Potential application of the Zürich–Montpellier system of vegetation description and classification in Australia. In *Vegetation Classification in Australia,* A. N. Gillison & D. J. Anderson, eds, ANU Press, Canberra, 1–9.

CHEAL, D. C., 1986. A park with a kangaroo problem. *Oryx* 20: 95–99.

CHEAL, D. C. & PARKES, D. M., 1989. Mallee vegetation in Victoria. In *Mediterranean Landscapes in Australia Mallee Ecosystems and their Management,* J. C. Noble & R. A. Bradstock, eds, CSIRO, East Melbourne, 125–140.

CHESTERFIELD, C. J. & PARSONS, R. F., 1985. Regeneration of three tree species in arid south-eastern Australia. *Australian Journal of Botany* 33: 715–732.

CHINNOCK, R. J., 1992. New taxa and combinations in the Myoporaceae. *Journal of the Adelaide Botanic Gardens* 15: 75–79.

COULSON, G., 1988. The history of kangaroo populations in Hattah–Kulkyne National Park, north-western Victoria. *Victorian Naturalist* 105 (4): 68–73.

CRISP, M. D., 1978. Demography and survival under grazing of three Australian semi-desert shrubs. *Oikos* 30: 520–528.

CUNNINGHAM, G. M., MULHAM, W. E., MILTHORPE, P. L. & LEIGH, J. H., 1981. *Plants of Western New South Wales.* NSW Government Printing Office, Sydney.

DOWNING, B. H., 1986. Goat and sheep grazing in shrub-infested semi-arid woodlands of New South Wales. *Australian Rangeland Journal* 8: 140–150.

FORAN, B. D., BASTIN, G., REMENG, E. & HYDE, K. W., 1982. The response to season, exclosure, and distance from water of three central Australian pasture types grazed by cattle. *Australian Rangeland Journal* 4: 5–15.

GARDINER, H. G., 1986. Dynamics of perennial plants in the mulga (*Acacia aneura* F. Muell.) zone of Western Australia. *Australian Rangeland Journal* 8: 18–27.

GRUBB, P. J. & HOPKINS, A. J. M., 1986. Resilience at the level of the plant community. In *Resilience in Mediterranean-Type Ecosystems*, B. Dell, A. J. M. Hopkins & B. B. Lamont, eds. W. Junk, Dordrecht, 21–38.

GULLAN, P. K., CHEAL, D. C. & WALSH, N. G., 1990. *Rare or Threatened Plants in Victoria.* Department of Conservation and Environment, Melbourne.

HALL, E. A. A., SPECHT, R. L. & EARDLEY, C. M., 1964. Regeneration of the vegetation on Koonamore Vegetation Reserve, 1926–1962. *Australian Journal of Botany* 12: 205–264.

HODGKINSON, K. C. & HARRINGTON, G. N., 1985. The case for prescribed burning to control shrubs in eastern semi-arid woodlands. *Australian Rangeland Journal* 7: 64–74.

HOLZAPPEL, C., SCHMIDT, W. & SHMIDA, A., 1992. Effects of human-caused disturbances on the flora along a Mediterranean-desert gradient. *Flora Morphologie Geobotanik Ökologie* 186: 261–270.

LAND CONSERVATION COUNCIL, 1987. *Report on the Mallee Area Review.* Land Conservation Council, Melbourne.

LAND CONSERVATION COUNCIL, 1989. *Mallee Area Review Final Recommendations.* Land Conservation Council, Melbourne.

LANGE, R. T. & GRAHAM, C. R., 1983. Rabbits and the failure of regeneration in Australian arid zone *Acacia. Australian Journal of Ecology* 8: 377–381.

LANGE, R. T. & PURDIE, R., 1976. Western myall (*Acacia sowdenii*), its survival prospects and management needs. *Australian Rangeland Journal* 1: 64–69.

MAGURRAN, A. E., 1988. *Ecological Diversity and its Measurement.* Princeton University Press, Princeton, New Jersey.

MITCHELL, A. A. & WILCOX, D. G., 1988. *Arid Shrubland Plants of Western Australia.* University of Western Australia Press, Perth.

ROSS, J. H., 1990. *A Census of the Vascular Plants of Victoria.* Department of Conservation and Environment, East Melbourne.

SQUIRES, V. R. & LOW, W. A., 1987. Botanical and chemical composition of the diet selected by cattle in three range types in central Australia. *Australian Rangeland Journal* 9: 86–95.

STORR, G. M., 1968. Diet of kangaroos (*Megaleia rufa* and *Macropus robustus*) and merino sheep near Port Headland, Western Australia. *Journal of the Royal Society of Western Australia* 51: 25–32.

WILLIAMS, O. B., 1969. Studies in the ecology of the Riverine Plain. 5. Plant density response of species in a *Danthonia caespitosa* grassland to 16 years of grazing by merino sheep. *Australian Journal of Botany* 17: 255–268.

WILLIS, J. H., 1972. *A Handbook to Plants in Victoria,* vol. 2. Melbourne University Press, Melbourne.

WILSON, A. D., 1979. Management of the natural pastures of south-western New South Wales. *Australian Rangeland Journal* 1: 351–362.

WILSON, A. D., MULHAM, W. E. & LEIGH, J. H., 1976. A note on the effects of browsing by feral goats on a belah (*Casuarina cristata*)—rosewood (*Heterodendrum oleifolium*) woodland. *Australian Rangeland Journal* 1: 7–12.

HOLOCENE VEGETATION AND ENVIRONMENTAL HISTORY OF CRANBOURNE BOTANIC GARDEN, VICTORIA

D. L. Aitken and A. P. Kershaw

Centre for Palynology and Palaeoecology, Department of Geography and Environmental Science, Monash University, Clayton, Victoria 3168

Aitken, D. L. & Kershaw, A. P., 1993:03:31. Holocene vegetation and environmental history of Cranbourne Botanic Garden, Victoria. *Proceedings of the Royal Society of Victoria* 105 (1): 67–80. ISSN 0035-9211.

The vegetation of the Cranbourne Botanic Garden has shown substantial changes during the Holocene due to the influences of climate, sea level rise, fire and, recently, European people. The earliest recorded phase, prior to 8,500 years BP, was characterised by ephemeral swamps and *Casuarina*-dominated dry-land communities. Climatic amelioration after this time is indicated by the establishment of permanent swamp conditions and an increase in *Eucalyptus* within the regional vegetation. Highest available moisture levels occurred between about 7,000 and 5,000 years ago as a result of increased effective precipitation and the attainment of high sea levels towards the end of the post-glacial marine transgression. *Casuarina* communities declined abruptly and were partially replaced by tall open eucalypt forests with a substantial amount of the wet sclerophyll taxon *Pomaderris* in the understorey. Increased climatic variability and burning within the last 5,000 years has led to the development of a diverse vegetation dominated by sclerophyll woodlands and heath which has been subsequently modified by European activities. These changes provide some basis for understanding the present nature and stability of the vegetation and should contribute to the formulation of future management practices.

IN 1970, the Royal Melbourne Botanic Gardens established an annexe at Cranbourne, now called the Cranbourne Botanic Garden, expressly for the purpose of cultivating and researching Australian native plants (Martin 1981, Pescott 1982). The annexe also incorporated a large, relatively undisturbed area of native heathland and *Eucalyptus* woodland, an important remnant of the vegetation that once covered an extensive area prior to clearing for agriculture and mining. The remnant vegetation provides the opportunity to conduct ecological research on *in situ* populations that could lead to the improvement of techniques for managing natural communities (Ashton 1987). The present project was designed to determine the current status of the vegetation from an examination of its history, providing information that might be of use in future management strategies. Specifically, the project involved the pollen analysis of accumulated swamp sediments within the Garden.

THE STUDY AREA

The Garden covers an area of approximately 350 hectares, 2.5 km to the south of the rapidly expanding township of Cranbourne at the extreme north of the Mornington Peninsula. The site is 50 km south-east of Melbourne and approximately 15 km from the shores of both Port Phillip Bay and Western Port (Fig. 1).

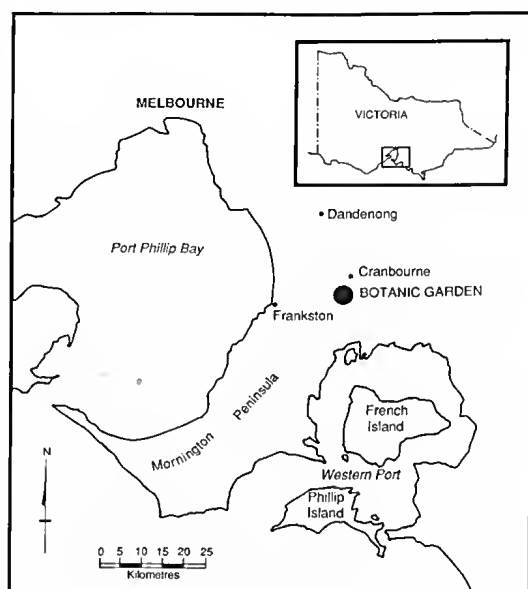The Cranbourne region is located in an area of Mediterranean climate with a maritime influ-

Fig. 1. Location of the study area.

ence (Conservation, Forests and Lands 1986, Pike & Calder 1978). Estimates from the climatic prediction system BIOCLIM (Booth et al. 1987) indicate that the garden receives an annual mean rainfall of about 800 mm of which 230 mm falls in the winter quarter and 160 mm in the summer quarter. The annual mean temperature is about 14° C, with a mean maximum temperature in the warmest month of 25° C and a mean minimum temperature in the coldest month of 6° C. Occasional winter frosts are experienced, and summer temperatures can exceed 30° C (Pike & Calder 1978). Winds are predominantly from the west and southwest quarters, tending from the north-west in summer.

The Garden lies about 60 m above sea level on a plain of low relief (Marsden et al. 1979). Most of the Garden is located on the Cranbourne Sand, a Pleistocene sand dune deposit, while Silurian siltstones and mudstones outcrop in the southern part. The well-drained dune crests support dry sandy podzols while the depressions, which are frequently seasonally wet, have humic podzol soils (Gullan 1978, Holmes et al. 1940). During high rainfall periods, temporary steams may develop in the interdune swamp areas. Loams, sandy loams and clay loams are the characteristic soil types on the Silurian rock areas.

Regionally, the vegetation was dominated by *Eucalyptus* forest and woodland before European settlement. To the north and north-east of the Garden were eucalypt woodlands with a grassy understorey (Holmes et al. 1940), while to the south and south-west *Eucalyptus cephalocarpa, E. radiata* and *E. viminalis* dominated open woodlands and open forests with *E. ovata* and *Melaleuca ericifolia* and/or *M. squarrosa* predominating in depressions or along stream-lines (Calder 1975). Wet sclerophyll forest elements such as *Pomaderris aspera, Olearia argophylla, Cyathea* and *Dicksonia* occurred to the north in the Dandenong Ranges and in sheltered gullies in the southern part of the Mornington Peninsula, while forests of *Banksia integrifolia* and *Casuarina stricta* were extensive in coastal areas. Indigenous vegetation today comprises only 15% of the land surface of the Mornington Peninsula (Calder 1975).

Gullan (1978) described and mapped the vegetation occurring predominantly on the Cranbourne Sands within the original annexe, before that area was augmented by additional land purchases (see Fig. 2). He identified four major

vegetation units. Unit 1 occurs on well-drained podzolic soils and is characterised by a sparse to dense canopy of *E. viminalis* with a variable understorey of *Leptospermum myrsinoides* and other heath species. On dune crests heath is dominant and *E. viminalis* often adopts a low mallee habit, while on the lower slopes, *E. viminalis* is taller and more abundant, often growing in association with *E. cephalocarpa*. Unit 2 occurs on low lying humic podzols and is dominated by a dense canopy of *E. cephalocarpa* and/or *E. viminalis* with a dense understorey composed of *Melaleuca squarrosa, Leptospermum juniperinum* and *Gahnia sieberana* in drier areas, and *Empodisma lateriflorus, Schoenus brevifolius, Lepidosperma longitudinale* and *Cassytha glabella* in wetter areas. Unit 3 is found on waterlogged humic podzols which inhibit the development of a tree layer. The dominant species here are the swamp sedges *L. longitudinale, Baumea tetragona* and *Chorizandra cymbaria*. On humic clay and other wet clayey soils, dense thickets of *M. squarrosa* predominate above a cover of sedges and rushes including *L. longitudinale* and *Lepyrodia muelleri* (Unit 4).

The original annexe area has been subjected to a number of disturbance factors including cattle grazing from the early 1820s, sand extraction since the early part of the present century and extensive vegetation clearing between 1966 and 1969 (Gullan 1978). Some small areas exist where vegetation is greatly disturbed resulting in mostly unvegetated sand. In the south and south-west the original vegetation has been entirely replaced by pasture. In the north-west, there remains an area of relatively undisturbed *E. radiata/E. cephalocarpa* open forest with an understorey of *Pteridium esculentum* and grasses. This is a remnant of the vegetation that was once widely distributed on Silurian sediments.

Prior to the arrival of Europeans, the region was inhabited by the Bunurong tribe who would have made extensive use of the area now occupied by the Garden, the sand ridges providing useful vantage points in the generally flat terrain and the swamps providing a range of plant and animal food resources (Ellender 1991). A recent brief archaeological survey of the Garden revealed a number of artefact scatters on the dunes surrounding one of the swamp sites used in this study (Ellender 1991).

Two swamp sites, unofficially named Tiger Snake Swamp and Tadpole Swamp on the basis of their most obvious faunal inhabitants, were
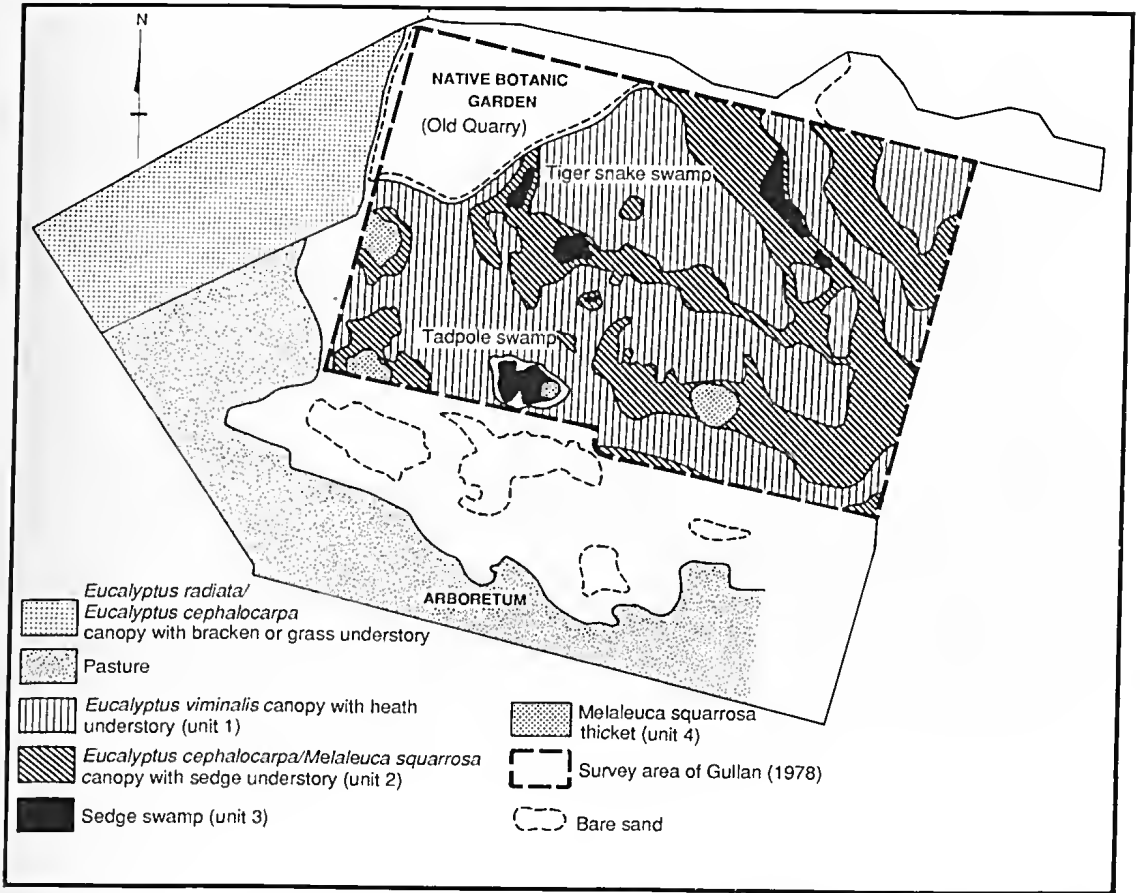
Fig. 2. Location of study sites and distribution of vegetation types within the Cranbourne Botanic Garden (after Gullan 1978; Royal Botanic Gardens aerial photo run 1989).

selected for study after preliminary coring of a number of potential sites in the Garden (Fig. 2).

Tiger Snake Swamp (Fig. 3) lies in an elongated basin approximately 100 m long and 30 m wide, situated to the south-east of a steep ridge of the main sand dune left undisturbed by local mining activities. From coring it was determined that the swamp lies in a shallow sandy depression perched on the clay sediments of the underlying Silurian mudstone. This depression forms a low spot along a more extensive drainage line between the north-west–south-east trending dune and the slightly elevated undulating land to the north-east. When visited in February and October 1990, the swamp contained between 60 and 100 cm of water but it is not known whether the surface dries out on oc-

casions. The swamp vegetation consists of scattered low shrubs of *M. squarrosa* growing out into the water and patchy distributions of species of Cyperaceae including *Lepidosperma longitudinale* and *Baumea tetragona*.

Around the swamp are thickets of *M. squarrosa* that are replaced on the slopes by open woodland of *E. viminalis* and *E. cephalocarpa*, with an understorey of *Pteridium esculentum* and heath, and on the ridges by low sandy heath. The sheltered south-facing slope of the dune supports a vigorous growth of *Gleichenia microphylla*, under a canopy of eucalypts on the middle slope and under *M. squarrosa* around the water's edge.

Tadpole Swamp (Fig. 4) is situated in a depression between the main dune ridge and a smaller sand accumulation to the south. The

Fig. 3. Tiger Snake Swamp and surrounding *Melaleuca squarrosa* thicket with *Gleichenia microphylla* and *Eucalyptus viminalis/E. cephalocarpa* woodland.

Fig. 4. Tadpole Swamp and surrounding *Melaleuca squarrosa* thicket with *Eucalyptus viminalis/E. cephalocarpa* woodland.

swamp is roughly rectangular in shape. Its open area measures approximately 85 m by 35 m, and adjacent *Melaleuca* scrub occupies a similar area. In December 1989 and in February 1990 the swamp surface was dry and cracking, but in October 1990 the basin contained about 1 m of water. From coring it was determined that the swamp lies in a sandy basin, but the underlying mudstone was not penetrated.

The swamp vegetation is very similar to that of Tiger Snake Swamp except for the presence of abundant *Villarsia exaltata* and *Triglochin procera*, and the substantial incursion of *M. squarrosa* over the swamp surface. Open *E. viminalis* and *E. cephalocarpa* woodland with an understorey of *P. esculentum, L. myrsinoides* and other heath species occurs on the dune slopes above the *M. squarrosa* thickets, while the upper slopes and dune crest are vegetated with heath, locally dominated by *L. myrsinoides.*

A major recent influence on Tadpole Swamp was a fire in April 1986 that burnt the surface peat and local vegetation, predominantly in the southern half of the swamp. Mining has not directly affected either site but an area immediately to the north of Tiger Snake Swamp and another to the south of Tadpole Swamp have been subject to extensive sand extraction.

FIELD AND LABORATORY METHODS

Core collection

Probing revealed that the deepest penetrable sediments occurred close to the centre of Tiger Snake Swamp. A 156 cm long core was extracted with a side filling peat sampler for subsequent analysis. The top 17 cm consisted of material too unconsolidated to be retained in the D-section sampler. This surface sediment was sampled with a PVC tube and stored in a freezer to prevent sediment mixing.

At Tadpole Swamp, probing indicated a depth of at least 2.5 m of penetrable sediment close to the centre of the basin. As the swamp surface was dry, a wide diameter core was collected in an 80 mm diameter PVC tube with the assistance of a piston attached to a tripod, and the core was extracted with a winch mechanism. The core was 241 cm in length.

Sediment description and sampling

In the laboratory, the stratigraphy of cores from both sites was described. Cores were then sampled for analysis by extraction of 1 cm slices

at regular intervals—5 cm for the Tadpole core, 4 cm for the Tiger Snake D-section core, and at contiguous 1 cm intervals for the frozen Tiger Snake core. In the freezer, the 17 cm core had shrunk to 14 cm. One cubic centimetre samples were then extracted from each slice for pollen and charcoal analysis. The remaining material was dried in an oven at 105° C for 24 hours and then ignited in a furnace at 500° C for 2 hours in order to determine moisture and organic contents.

Pollen and charcoal sample preparation

Preparation of samples for pollen and charcoal analysis followed standard methods detailed by Faegri & Iversen (1975). These included potassium hydroxide treatment to break down the sediment and dissolve fine humic material, sieving to remove larger plant fragments and sand, hydrofluoric acid treatment to dissolve silicates, and acetolysis to dissolve additional organic matter and darken the pollen grains to facilitate identification. Prepared samples were mounted on microscope slides in a measured quantity of silicone oil.

Counting and identification

Using an Olympus CHA microscope at 300 × or 600 × magnification, pollen grains were counted along evenly spaced transects across each slide until 150 grains of dry-land plants had been recorded. Identification was generally only possible to the genus or family level, but many fern spores that had lost their exosporia could only be counted as monolete or trilete morphological types. Except for *Leptospermum*, there was difficulty in separating many myrtaceous grains to lower taxonomic levels, so that there may be some overlap in identifications between the broad categories *Eucalyptus*-type, *Melaleuca*-type and myrtaceous shrubs. A distinctive Asteraceae grain with very blunted spines was given its geological form taxon name *Tubulifloridites pleistocenicus* (Martin 1973), while *Myriophyllum* was sub-divided on the number of grain apertures.

All black, opaque, angular particles over 15 μm maximum diameter were deemed to be charcoal derived from the burning of plant material. These were also counted along spaced transects. All samples from Tadpole Swamp and the frozen core from Tiger Snake Swamp were counted but, due to time constraints and the sparse and poorly preserved nature of grains

from the Tiger Snake peat sampler core, only a few samples were examined from there.

Radiocarbon dating

Samples were submitted for dating to the Radiocarbon Laboratory, University of Waikato. Initially, samples were selected from the bases of the more organic-rich sediments in each core, i.e. 160–156 cm at Tadpole Swamp and 70–69 cm at Tiger Snake Swamp. Subsequently, samples were submitted from depths of 105–100 cm and 65–60 cm in the Tadpole Swamp core in order to date significant changes in the pollen record.

POLLEN DIAGRAMS

Tadpole Swamp (Fig. 5)

The Tadpole Swamp diagram has been divided into zones on the basis of major changes in representation of dry-land pollen taxa. Pollen and charcoal concentrations vary dramatically through the sequence. Pollen concentrations tend to peak at or close to zone boundaries while highest values for charcoal occur at the very base of the sequence and in Zone T4.

Zone T1 (200–160 cm), > c. 8,500 BP. The pollen record begins where organic matter in the form of macroscopic plant remains becomes visible within the basically sandy sediments. Throughout the zone both moisture and organic contents of the sediment are low. Aquatic pollen is dominated by three taxa, Melaleuca-type, Cyperaceae and Haloragis, with Restionaceae, Typha, Sphagnum and Tiletia, the fungal associate of Sphagnum being less common or rare. Baumea appears close to the top of the zone. Dry-land pollen is dominated by Casuarina, with Eucalyptus-type, Leptospermum, Poaceae and Trachymene having moderate values. The only other taxa with a notable presence are myrtaceous shrubs, Asteraceae (Tubuliflorae), Tubulifloridites pleistocenicus, Chenopodiaceae and trilete fern spores.

Zone T2 (160–100 cm), c. 8,500–7,000 BP. At the base of this zone there is a sharp increase in both moisture and organic contents of the sediment, and peat becomes the dominant sediment type. Within the aquatic assemblage Baumea is the most important taxon. Restionaceae values have increased, while Melaleuca-type, Cyperaceae and particularly Haloragis have significantly reduced percentages. Myriophyllum has its only occurrences in this zone. Of the dry-land

taxa, Casuarina continues to dominate, with substantially increased values for Poaceae and a slight increase in Eucalyptus-type. All other taxa, apart from Pteridium, have poor representation.

Zone T3 (100–70 cm), c. 7,000–5,000 BP. There is no change in the nature of the sediments through the zone except for slight declining trends in moisture and organic contents, which continue to decline gradually as far as the sediment surface. Values for Cyperaceae and Baumea are generally lower than in the previous zone, while Melaleuca-type and Restionaceae increase towards the top of the zone. Tiletia shows an isolated large peak at the T2–T3 zonal boundary, while Sphagnum shows two high values within the zone. The dry-land taxon Casuarina declines dramatically through the zone, while Eucalyptus-type continues to increase so as to form the major dry-land pollen component. Poaceae maintains its relatively high representation while Pomaderris and Amperea have their highest values for the diagram. Chenopodiaceae and Asteraceae (Tubuliflorae) have higher representation than in the previous zone and Leptospermum and myrtaceous shrub values increase through the zone to levels present in Zone T1. All pteridophyte taxa are poorly represented.

Zone T4 (70–0 cm), c. 5,000–present. The aquatic pollen record is dominated by Melaleuca-type, Baumea, Restionaceae and Sphagnum, with Cyperaceae decreasing towards the surface to its lowest levels for the diagram. Haloragis almost disappears after a relatively high value in the basal sample, while Villarsia is consistently present in the upper part of the zone. Leptospermum is the dominant dry-land taxon, while Eucalyptus-type declines abruptly at the T3–T4 zonal boundary. Casuarina, Eucalyptus-type and Poaceae are moderately abundant. Plantago (native) and Monotoca are consistently present for the first time, the latter together with Pomaderris achieving high values in the top two samples. Pteridophytes are better represented than in lower zones, with both Pteridium and trilete fern spores having occasional high values. The presence of Pinus in the top sample suggests that this sample falls within the period of European occupation.

Tiger Snake Swamp (Fig. 6)

D-section core sequence (80–20 cm). The pollen record begins above the basal clay and the lower part of the organic sand. Initially both water and
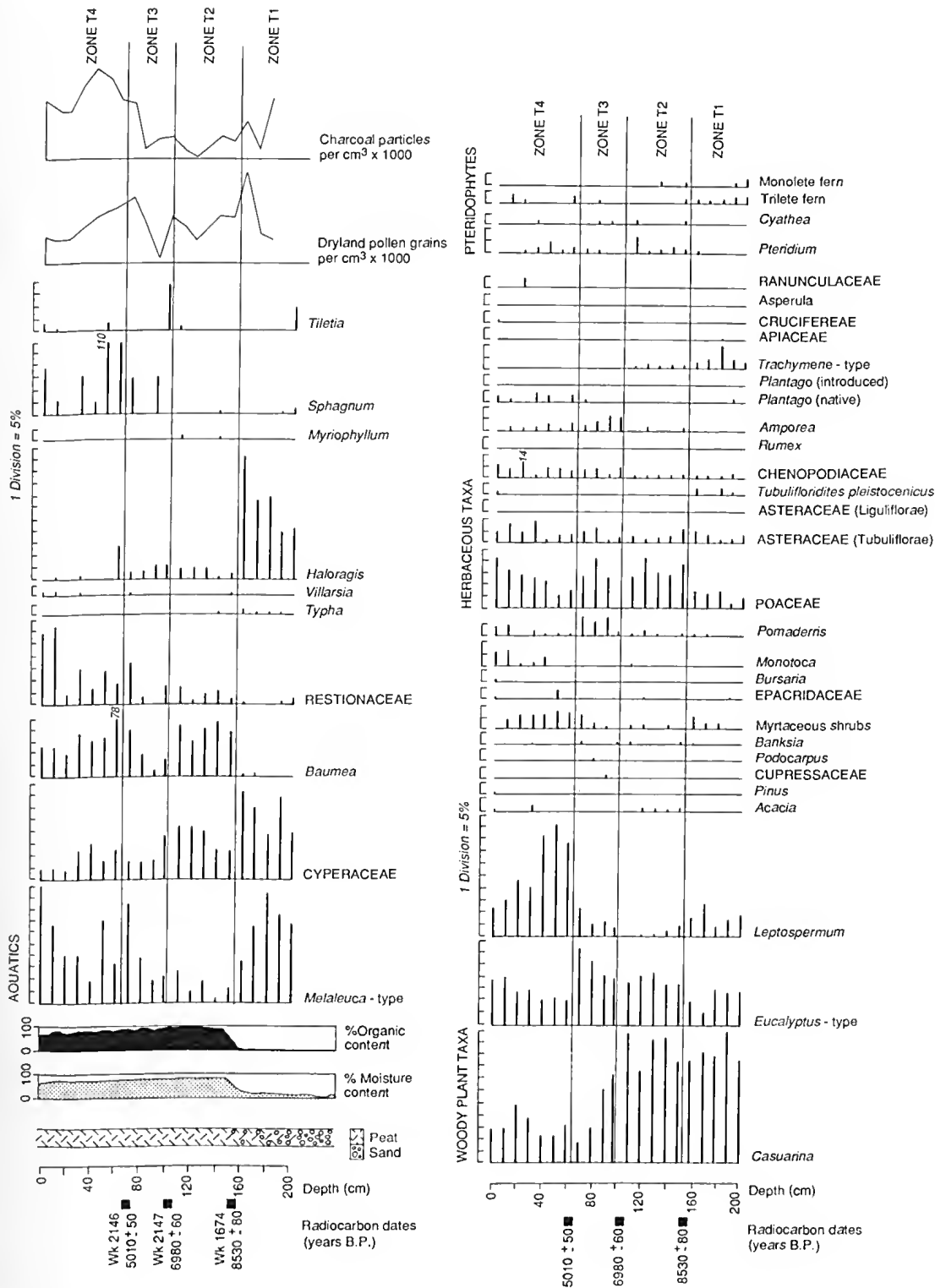
Fig. 5. Pollen diagram from Tadpole Swamp. Values for all pollen taxa expressed as percentages of the native dry-land plant pollen sum for each sample.

organic contents are very low, but water content increases from about 60 cm to the surface and organic content becomes marginally higher in the top 40 cm.

The pollen spectra have high representation of a number of aquatic taxa. *Melaleuca* achieves extremely high values in the interval before the radiocarbon date of 5,500 years BP, whereas Restionaceae and *Sphagnum* peak after this time. *Typha, Myriophyllum* and *Haloragis* show consistent representation while *Villarsia, Triglochin* and *Tiletia* are present at some levels. Pore number variation in *Myriophyllum* appears extremely variable but this is caused largely by very low pollen representation in some samples. In general terms, the proportion of 5–7 pored specimens decreases through the sequence.

Dry-land pollen spectra are dominated by *Casuarina* except in two samples around the date of 5,500 BP where *Eucalyptus* achieves highest values. Other well represented taxa include Poaceae, *Leptospermum, Pteridium* and Asteraceae, with both Asteraceae (Tubuliflorae and *Tubulifloridites pleistocenicus*) peaking along with *Eucalyptus* at the expense of *Casuarina* at 70 cm. Epacridaceae, *Pomaderris,* myrtaceous shrubs, *Monotoca,* Chenopodiaceae, *Amperea, Plantago* (native), Cruciferae, *Gleichenia* and trilete spores are the only other taxa with more than a single occurrence. *Pinus* is present in the top sample.

Pollen concentrations are relatively consistent through most of the sequence but decline substantially towards the top and were insufficient to obtain a statistically meaningful count at 28 cm. Charcoal values fluctuate throughout.

Frozen core sequence (14–0 cm). Moisture and organic contents are generally higher than in the D-section core and the closer sampling interval allows a better assessment of pollen changes. In contrast to earlier spectra, *Myriophyllum* dominates the basal part of this sequence from 14–6 cm, although the other major aquatics *Melaleuca,* Cyperaceae, *Baumea,* Restionaceae and *Sphagnum* also have relatively high values. All these taxa together with *Typha* decrease in the uppermost samples, while *Villarsia* disappears. Only *Haloragis* maintains its percentages.

Within the dry-land taxa there is higher diversity than in the D-section core sequence, with a number of native taxa including *Callistemon, Banksia, Acacia,* Proteaceae, *Leucopogon* and *Dicksonia* being represented for the first time and significant increases in values for *Monotoca, Pomaderris,* Chenopodiaceae, *Plantago*

(native), *Cyathea* and other pteridophyte spores. From the basal sample of this sequence, *Casuarina* declines relative to *Eucalyptus* and then falls dramatically in the top three samples. This fall is accompanied by a substantial increase in Poaceae and a lesser increase in *Leptospermum. Pteridium* also declines in the top samples while *Gleichenia* increases. The impact of Europeans is indicated by relatively high values for the exotics *Pinus,* Asteraceae (Liguliflorae) and *Plantago* (introduced), and the probable exotics *Rumex* and *Apiaceae.* There is some indication of the replacement of native *Plantago* by introduced species in the top few samples.

Pollen concentrations are constant at moderate levels while charcoal values increase initially and then decline sharply in the top few samples.

DISCUSSION

Site record correlation

The radiocarbon dates suggest that the Tiger Snake Swamp record may only cover the period represented by Zone T4 and the upper part of Zone T3 in the Tadpole Swamp record. Some additional support for this conclusion is provided by similar changes in some dry-land pollen taxa. *Casuarina* shows a marked decline around the radiocarbon age of 5,000–5,500 BP in both records while Poaceae values dip after this level in both diagrams. There are also marked differences between the two records, however, particularly in samples dating older than 5,500 BP. In these samples, the record from Tiger Snake Swamp has much lower values for *Eucalyptus* and Asteraceae, and higher percentages for *Leptospermum* and *Pteridium,* in these respects more closely resembling lower samples from Tadpole Swamp. Similarly, the high values of *T. pleistocenicus* at the base of the Tiger Snake Swamp core suggest an age older than 8,500 BP, although this is not supported by the relatively high values for *Amperea.* It is possible that hiatuses may be present in the Tiger Snake Swamp record or that there has been mixing of the older sediments. Alternatively, there may have been a high degree of heterogeneity in the vegetation and differential response to environmental changes, thus inhibiting clear biostratigraphic correlation. The aquatic taxon values in the two records differ considerably, preventing correlation on those data.

The first appearance of *Pinus* is noted in the top sample of Tadpole Swamp and at 20 cm
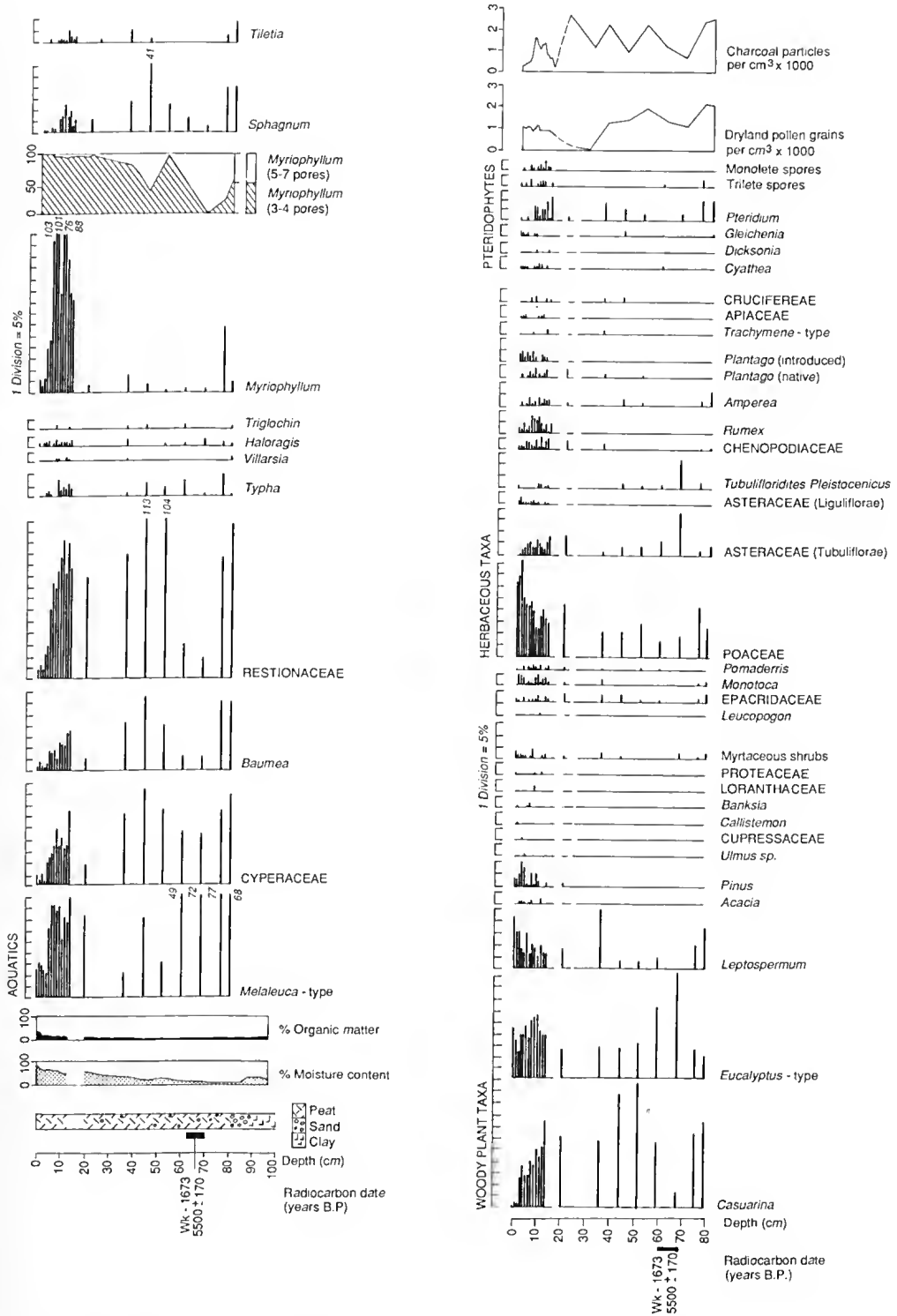
Fig. 6. Pollen diagram from Tiger Snake Swamp. Values for all pollen taxa expressed as percentages of the native dry-land plant pollen sum for each sample.

depth at Tiger Snake Swamp. It is thus likely that there has been little sediment accumulation since European settlement, or that those sediments were burnt in the fire of April 1986 at Tadpole Swamp.

For the purpose of vegetation and environmental reconstruction, most attention will be paid to the more detailed record from Tadpole Swamp for the pre-European period, and to the frozen core record from Tiger Snake Swamp for the European phase.

The hydroseral record

Organic sedimentation in Tadpole Swamp commenced in the early Holocene, probably between 10,000 and 9,000 years ago. Before that time conditions were likely to have been too dry to support swamp or open-water environments. During the early Holocene, precipitation had increased sufficiently to allow the formation of a swamp supported directly by precipitation or, more likely, by a rise in the regional water table resulting from the wetter conditions. The combination of high values for Cyperaceae, *Haloragis* and *Melaleuca*-type indicates an herbaceous swamp surrounded by *Melaleuca* thickets. The inorganic nature of the sediments suggests some environmental variability, most probably regular drying of the swamp surface causing oxidation of accumulated organic sediments. It is also possible that there was still some sand mobility under an incompletely vegetated dune cover.

Permanently wet conditions are indicated after 8,500 BP with the accumulation of organic-rich sediments. Water levels increased, reducing the extent of marginal *Melaleuca* thicket, and the herbaceous swamp became more diverse with the addition of *Baumea* and Restionaceae. The lack of an inorganic substrate would have limited the extent of *Typha*. It is likely that some open water, colonised by the submerged aquatic *Myriophyllum*, also existed.

About 7,000 BP *Sphagnum*, which had always been present on site, expanded and the herbaceous fen component was reduced. This vegetation change may represent a succession from fen to bog as a result of sediment accumulation, although the change corresponds with a similar change in dry-land vegetation suggesting that regional climatic change could have been a contributing factor. More extensive bog development, combined with expansion of *Melaleuca* from towards the end of the period represented by Zone T3, is more obviously a successional

development, perhaps facilitated by generally drier conditions.

A similar mix of aquatics to that at Tadpole Swamp was present at Tiger Snake Swamp during the period represented in the D-section core, although clear patterns are difficult to discern. The presence of *Myriophyllum* in addition to the various emergent herbs, *Sphagnum* and *Melaleuca* suggests a rather unstable mosaic of open water, fen, bog and thicket. The low organic content of the sediment indicates frequent surface drying which created sufficient instability to prevent any directional successional change.

There are two possible causes of this instability. One possibility is that Tiger Snake Swamp, lying within an old drainage line, has been influenced by intermittent and erosive stream flow. This could explain the relatively high inorganic content of the sediment resulting in dilution of accumulated organic material from the remains of swamp plants, and perhaps the variability in dry-land as well as in aquatic pollen composition. It might also explain why the pollen record dates only from about 6,000 years ago as before that time, when precipitation was likely to have been higher than today, water flow could have prevented deposition or removed the finer organic component of the sediment that included the pollen. An alternative explanation is that the swamp has always been ephemeral, and its drying out at regular intervals would have resulted in oxidation of accumulated organic material. The formation of a swamp environment suitable for pollen preservation might have resulted from a rise in the regional water table as sea level reached its present level about 6,000 years ago. The fact that there has been a similar sediment accumulation rate at both Tiger Snake Swamp and Tadpole Swamp within the last 5,000–6,000 years, despite the very different nature of the sediments, suggests a strong regional water table control over swamp development during this period.

Major hydrological changes appear to have accompanied European arrival. At Tiger Snake Swamp there was a massive increase in *Myriophyllum* pollen. The change in *Myriophyllum* pore ratio also suggests a change in floristic composition. A similar increase in *Myriophyllum* pollen representation since European occupation has been noted elsewhere in Victoria and tentatively attributed to catchment disturbance resulting in increased hydrological variability (Kershaw & Gell 1990). The high pollen percentages of *Myriophyllum* may not indicate a substantial increase in abundance of parent plants

but could result from more frequent swamp drying, as many species of *Myriophyllum* only flower when stranded (Orchard 1986). The parallel decrease in pollen of all aquatic taxa within the top few samples is difficult to interpret. It may reflect increased pollen influx from dryland vegetation rather than an overall reduction in aquatic plants or their flowering.

There is little evidence of the European phase of Tadpole Swamp but the present abundance there of *Triglochin*, which at Tiger Snake Swamp is only recorded before European occupation, suggests that floristic changes have also taken place here.

The dry-land record

Casuarina was clearly the regional dominant during the early Holocene. Although it is not possible to be certain of component species, the size range of pollen grains represented suggests that the woodland taxa *C. stricta* and *C. littoralis* as well as heath species such as *C. pusilla* and *C. paludosa* were present. It is likely that the major vegetation type was *Casuarina* woodland or forest containing a significant proportion of eucalypts. Low values for low-growing taxa that have significant pollen dispersal, such as Poaceae, Asteraceae, Chenopodiaceae and *Pteridium*, suggest that the understorey was fairly sparse. This kind of vegetation was a feature of much of lowland Victoria during the early Holocene (D'Costa et al. 1989), but the reason for the importance of *Casuarina* as opposed to *Eucalyptus*, the canopy dominant of forests and woodlands today, has not been established. It could be due to the ability of *Casuarina* to colonise faster than eucalypt species after the last glacial period when herbaceous steppe vegetation dominated the region, to a climate that was more suitable for *Casuarina*, or to less intense burning (D'Costa et al. 1989). There is little information in the records from Tiger Snake and Tadpole swamps to help clarify the issue. Prior to 8,500 BP the climate was certainly drier than at present, as indicated by the ephemeral nature of Tadpole Swamp, but *Casuarina* maintained its dominance, albeit with some increase in *Eucalyptus* together with the understorey taxa Poaceae and *Pteridium*, under precipitation levels that were probably as high as those of today until its major decline around 7,000 BP. The charcoal record is much too variable to allow any assessment of the likely role of fire in this *Casuarina* decline.

The lower Holocene around Tadpole Swamp is also characterised by the significant representation of *Tubulifloridites pleistocenicus* and *Trachymene*-type, and the former survived into the late Holocene, being present in both diagrams within the European phase. Both these taxa are common components of cooler environments, *T. pleistocenicus* frequently dominating glacial assemblages (Kershaw et al. 1991). These taxa may have survived from the last glacial period in this area.

There has been discussion on the likely parent plants of *T. pleistocenicus* (Martin 1986, D'Costa & Grindrod 1991, Macphail & Martin 1991). Only two species, *Calomeria amaranthoides* Vent and *Cassinia arcuata* R. Br., have been identified in south-eastern Australia as having the same type of pollen (Macphail & Martin 1991). *C. arcuata* is presently recorded from the Cranbourne Botanic Garden and is almost certainly the pollen source in the surface samples. Whether this species was the parent plant of the older pollen is debatable, as there is a gap in representation of this pollen type even at Tiger Snake Swamp where it appears to extend into the middle-upper Holocene. At no site in south-eastern Australia is *T. pleistocenicus* recorded in more than trace values in recent times, so it would appear that no vegetation analagous to that containing high levels of this taxon from older periods presently exists. Either one or both of the identified extant species had a very different ecology in the past, or other plants which are now extinct were the source of the Pleistocene or early Holocene pollen.

Support for the evidence derived from the aquatic diagram of high water levels between 8,500 and 5,000 BP is provided by reduced values of *Leptospermum* and myrtaceous shrubs, which are likely to have been growing locally as their pollen is poorly dispersed. These may have formed part of the swamp fringe, together with *Melaleuca* which may have retreated as a result of higher water levels. Highest effective precipitation probably occurred between 7,000 and 5,000 years ago with the maximum expansion of the wet sclerophyll taxon *Pomaderris*. This expansion corresponds very closely with a similar peak in *Pomaderris* in diagrams from the Gippsland Lakes (Hooley et al. 1980) and with the period of highest lake levels in the Western Plains volcanic crater lakes, as determined from sedimentological, microfaunal and microfloral evidence (Bowler & Hamada 1971, Dodson 1974, De Deckker 1982).

Abrupt increases in *Amperea* and Chenopodiaceae also occured around 7,000 years ago. As both these taxa have significant representation

in near-coastal environments, their expansion may have been related to the closer proximity of the sea towards the end of the post-glacial marine transgression. Certainly, sea level stabilisation could have resulted in habitats suitable for salt marsh colonisation and, as the chenopodiaceous dominants of these communities have well dispersed pollen, they could have contributed a significant regional pollen component. *Amperea* is essentially a dune inhabitant that exists today within the Garden. Any effect on its distribution or abundance resulting from the proximity of the sea would have been less direct.

After 5,000 years ago the vegetation became more diverse with increased representation of understorey taxa relative to *Eucalyptus*. As suggested previously, the large increases in *Leptospermum* and myrtaceous shrubs can be explained by an invasion of the swamp surface as a result of lower water tables, but the addition of *Monotoca* suggests a general expansion of heath vegetation. It is likely that the eucalypt canopy became more open with an understorey mosaic of heath, *Pteridium* and grassland. This diversity may have been the result of increased burning as indicated by relatively high charcoal levels. Conditions responsible for more frequent fires may have been anthropogenic or climatic. Archaeologists have argued that there was intensified occupation of Australia, together with increased use of fire, within the last 4,000–5000 years (Head 1989, Hughes & Sullivan 1981), while McGlone et al. (1992) have suggested that increased burning could have been caused by an intensification of El Niño–southern oscillation-related climatic variability accompanied by lower rainfall from 5,000 to 6,000 years ago.

A further increase in disturbance levels is reflected in vegetation changes during the period of European occupation, as indicated in the frozen core sequence from Tiger Snake Swamp. The major feature is the addition of exotics. *Pinus* is probably derived from plantations and other plantings outside the Garden, but a significant proportion of the pollen from *Rumex, Plantago* (exotic) and Asteraceae (Liguliflorae) could have been from more local sources. There is some indication that native Asteraceae and *Plantago* are being replaced by their exotic counterparts. Within the native woody plant component, shrubs and small trees of *Acacia, Banksia* and *Monotoca* have higher values, indicating an increase in shrub understories of the woodlands, or the replacement of woodlands by shrubland and heath. The general increase in

grasses partially reflects clearing of surrounding vegetation. There is a significant increase in trilete and monolete fern species, probably due to hydrological changes around the margins of the swamp.

The taxa most adversely affected by European activities appear to be *Pteridium* and *Casuarina*, both of which show a marked decline in the top three samples. The substantial increase in Poaceae in these samples suggests that an acceleration in vegetation clearance has been important, perhaps targeting those communities containing significant proportions of these taxa.

The effect of fire on vegetation changes since European occupation is difficult to gauge. It would appear that burning levels have been reduced from pre-European times, but the generally lower pollen densities suggest that charcoal particle concentrations have been effectively diluted by an increase in the rate of sediment accumulation. The peaks in charcoal at the top of the Tadpole Swamp and Tiger Snake Swamp cores, which record the first evidence of exotics, might be significant. Here, pollen concentrations are low suggesting real increases in charcoal that might indicate intense burning during early days of colonisation. Similarly, the real decrease in charcoal within the top three samples of the Tiger Snake frozen core may reflect the policy of deliberate fire exclusion and may date from the widespread fires of 1939. Accelerated clearing during this period would have assisted fire reduction in that the ignition source area would have been substantially reduced.

CONCLUSIONS

Two sites from the Cranbourne Botanic Garden together provide a record of changing vegetation and environments from about the beginning of the Holocene to the present day. Prior to 8,500 years ago, swamps were ephemeral and the regional vegetation was composed largely of open woodland or forest dominated by *Casuarina*, under effective precipitation levels lower than those of today. Some communities characteristic of the preceding cool dry glacial period may also have survived.

The development of permanent swamp conditions about 8,500 years BP indicates an increase in moisture levels. *Casuarina* was gradually replaced by *Eucalyptus* as the dry-land canopy dominant, with high levels of *Pomaderris* between 7,000 and 5,000 years BP indicating a regional expansion of tall open or wet sclero-

phyll forest under maximum Holocene precipitation. High precipitation and high water table levels after 7,000 years BP may have resulted from the close proximity of the sea as sea level reached almost its present height.

After 5,000 years BP there is evidence for increased climatic variability and for increased burning. The vegetation became more diverse with the addition of a significant heath component. This trend was accelerated under higher levels of disturbance resulting from the impact of European people.

The record illustrates and helps to refine the dating of a number of features of Holocene environments in Victoria. These include an early domination by *Casuarina* and its subsequent decline, a peak in precipitation and maximum *Pomaderris* expansion in the mid-Holocene, and increased climatic variability and/or disturbance to the vegetation in the late Holocene.

The record might also contribute to future management of the indigenous vegetation of the Cranbourne Botanic Garden. It illustrates that the vegetation, both aquatic and dry-land, responds markedly to changes in climate, and this has major implications for likely future changes under predicted Greenhouse climates. The general trend throughout the Holocene has been one of increasing diversity which has never been higher than at present. Much of this diversity has resulted from relatively high levels of disturbance reflected mainly in the form of increased burning, and clearly fire must be seen as an integral part of any management strategy. Particular care must be taken to protect some components of the system that have declined substantially in recent times. These components include *Casuarina*, which must be regarded as having relict status, and native *Plantago* and Asteraceae, which appear to be being replaced by exotic relatives.

Further useful information that would contribute to an assessment of the present status of the vegetation and its future management could be obtained by a temporally precise palynological study of the last few hundred years, incorporating refined taxonomic identification, charcoal counting and dating methods.

ACKNOWLEDGMENTS

REFERENCES

ASHTON, P. S., 1987. Biological considerations in *in situ* versus *ex situ* plant conservation. In *Botanic Gardens and the World Conservation Strategy*, D. Bramwell, D. Hamann, V. Heywood & H. Singe, eds, IUCN/Academic Press, London, 117–130.

BOOTH, T. H., NIX, H. A., HUTCHINSON, M. F. & BUSBY, J. R., 1987. Grid matching: a new method for home cline analysis. *Agriculture and Forest Meteorology* 39: 241–255.

BOWLER, J. M. & HAMADAT, T., 1971. Late Quaternary stratigraphy and radiocarbon chronology of water level fluctuations in Lake Keilambete, Victoria. *Nature* 232: 330–332.

CALDER, W., 1975. *Peninsula Perspectives: Vegetation on Mornington Peninsula, Victoria*. Centre for Environmental Studies, University of Melbourne.

D'COSTA, D. M., EDNEY, P., KERSHAW, A. P. & DE DECKKER, P., 1989. Late Quaternary palaeoecology of Tower Hill, Victoria. *Biogeography* 16: 461–482.

D'COSTA, D. M. & GRINDROD, J., 1991. "Spineless" Asteraceae. *Palynological and Palaeobotanical Association of Australasia Newsletter* 22: 9.

DE DECKKER, P., 1982. Holocene ostracods, other invertebrates and fish remains from cores of four maar lakes in southeastern Australia. *Proceedings of the Royal Society of Victoria* 94: 183–220.

DODSON, J. R., 1974. Vegetation and climatic history near Lake Keilambete. *Australian Journal of Botany* 22: 709–710.

ELLENDER, I., 1991. Aboriginal archaeological sites in the Royal Botanic Gardens, Cranbourne. Unpublished report, Victorian Archaeological Survey.

FAEGRI, K. & IVERSEN, J., 1975. *Textbook of Pollen Analysis*, 3rd edn. Blackwell, Oxford.

GULLAN, P. K., 1978. Vegetation of the Royal Botanic Gardens Annexe at Cranbourne, Victoria. *Proceedings of the Royal Society of Victoria* 90: 225–240.

HEAD, L., 1989. Prehistoric Aboriginal impacts on Australian vegetation: an assessment of the evidence. *Australian Geographer* 20: 37–46.

HOLMES, O. C., LEEPER, G. W. & NICHOLLS, R. D., 1940. Soil and land utilization survey of the country around Berwick. *Proceedings of the Royal Society of Victoria* 52: 177–245.

HOOLEY, A. D., SOUTHERN, W. & KERSHAW, A. P., 1980. Holocene vegetation and environments of Sperm Whale Head, Victoria. *Journal of Biogeography* 7: 349–362.

HUGHES, P. J. & SULLIVAN, M. E., 1981. Aboriginal burning and late Holocene geomorphic events in eastern NSW. *Search* 12: 277–278.

KERSHAW, A. P. & GELL, P. A., 1990. Quaternary vegetation and the future of the forests. In *Lessons for Human Survival: Nature's Record from the Quaternary*, P. Bishop, ed., Geological Society of Australia Symposium Proceedings 1, 11–20.

KERSHAW, A. P., D'COSTA, D. M., MCEWAN MASON, J. & WAGSTAFF, B. E., 1991. Quaternary vegetation of mainland southeastern Australia. *Quaternary Science Reviews* 10: 391–404.

MARSDEN, M. A. H., MALLETT, C. W. & DONALDSON, A. K., 1979. Geological and physical setting, sediments and environments, Western Port, Victoria. *Marine Geology* 30: 11–46.

MACPHAIL, M. K. & MARTIN, A. H., 1991. "Spineless" Asteraceae II. *Palynological and Palaeobotanical Association of Australasia Newsletter* 23: 1–2.

MCGLONE, M., KERSHAW, A. P. & MARKGRAF, V., 1992. El Niño–southern oscillation and climatic variability in Australasian and South American palaeoenvironmental records. In *Historical and Palaeoclimatic Aspects of the Southern Oscillation*, H. F Diaz & V. Markgraf, eds, Cambridge University Press, 435–462.

MARTIN, A. R. H., 1986. Late glacial and early Holocene vegetation of the alpine zone, Kosciusko National Park. In *Flora and Fauna of Alpine Australasia: Ages and Origins*, B. A. Barlow, ed., CSIRO, Melbourne, 161–172.

MARTIN, H. A., 1973. Palynology of some Tertiary and Pleistocene deposits, Lachlan River valley, New South Wales. *Australian Journal of Botany, Supplementary Series* 6: 1–57.

MARTIN, S. D., 1981. Development of a native Botanic Garden at Cranbourne. *Australian Parks and Recreation*, May: 1–35.

ORCHARD, A. E., 1986. *Myriophyllum* (Haloragaceae) in Australia. II. The Australian species. *Brunonia* 8: 173–291.

PESCOTT, R. T. M., 1982. *The Royal Botanic Gardens, Melbourne: A History from 1845 to 1970*. Oxford University Press, Melbourne.

PIKE, J. & CALDER, W., 1978. *Frankston–Baxter Corridor Study, Stage One Report*. Centre for Environmental Studies. University of Melbourne.

TWO NEW SPECIES OF HALECIIDAE (HYDROZOA: HYDROIDA) FROM SOUTHERN AUSTRALIA

Jeanette E. Watson

Honorary Associate, Museum of Victoria, 285 Russell Street, Melbourne, Victoria 3000

Two new species of Haleciidae are described from southern Australia. *Halecium amphibolum* sp. nov. is a seagrass epiphyte and *Campalecium alcoicum* sp. nov. is epizoic on a crustose bryozoan. The latter species is the first record of *Campalecium* from Australia.

TWO new species of hydroids referrable to the family Haleciidae were found during ecological studies in Port Phillip Bay, Victoria. One of the species, belonging to *Halecium*, occurs in the epiphytic hydroid community of the seagrass *Amphibolis antarctica* (Labill.) Sonder & Aschersen at Queenscliff, near Port Phillip Heads. The other species, belonging to *Campalecium*, is epizoic on a crustose bryozoan growing on a jetty in shallow water. It is the first record of *Campalecium* from Australia.

Type material lodged in the Museum of Victoria is denoted by the prefix NMV.

Family Haleciidae Hincks, 1868

Halecium amphibolum sp. nov.

Fig. 1A–D

Etymology. The specific name refers to the host plant.

Type material. Holotype NMV F59426, microslide, female colony from *Amphibolis antarctica*, 3 m, Queenscliff, Victoria, coll. J. E. Watson, 16 Nov. 1986. Paratype NMV F59427, male colony (formalin preserved) on *Amphibolis antarctica*, 3 m, Queenscliff, Victoria, coll. J. E. Watson, 24 Jun. 1986.

Description. Colonies consisting of up to six small, branched stems.

Hydrorhiza tubular, thick and robust, 0.1 mm in width, adherent to seagrass leaf. Stems short, unfascicled, up to 6 mm in height, taller stems bearing several hydrothecae but many hydrothecae borne directly on hydrorhiza. Perisarc of primary stem or pedicel thick, with at least three deep proximal annulations above junction with hydrorhiza, these continuing into distal region but sometimes fading into smooth perisarc. Primary pedicel straight, 0.3–0.7 mm long, proximal width 0.08–0.14 mm, distal width below hydrotheca 0.12–0.15 mm, secondary and later pedicels arising from geniculation just below primary hydrophore. Branching sympodial to roughly dichotomous, occurring below proximal hydrotheca on older stems.

Hydrotheca deep, not sessile, expanding to margin. Margin at right angles to axis of pedicel, strongly everted, with outrolled rim, width 0.18–0.23 mm, diaphragm distinct, width 0.11–0.13 mm, depth from margin to diaphragm 0.05–0.08 mm, a few desmocytes visible in empty hydrothecae. Up to three hydrothecal replications common in older stems, replicated hydrothecae given off from diaphragm of preceding one, pedicel short to absent. Hydranth large, robust, with about 20 tentacles.

Colonies dioecious. Gonothecae of both sexes similar in overall shape and size, irregularly ovate, laterally flattened, length 0.7–0.9 mm, maximum width 0.5–0.8 mm, perisarc smooth, borne on short, thick pedicel 0.10–0.15 mm long, arising below a hydrotheca on proximal stem region or from hydrorhiza. Aperture of male gonotheca circular, 0.17–0.20 mm wide, with small upraised collar distally situated on one side of capsule, spermatogenic mass contained within reticulated spadix. Aperture of mature female gonotheca an angular notch in summit; gonophore containing up to eight large ova.

Perisarc of colonies honey-coloured, hydranths yellow, gonophores creamy-pink, aperture of gonotheca dark brown.

Remarks. In size of colony, *Halecium amphibolum* sp. nov. resembles some of the smaller species of Haleciidae such as *H. pusillum* Sars, 1857, *H. nanum* Alder, 1859 and *H. corrugatissimum* Trebilcock, 1928. However, careful
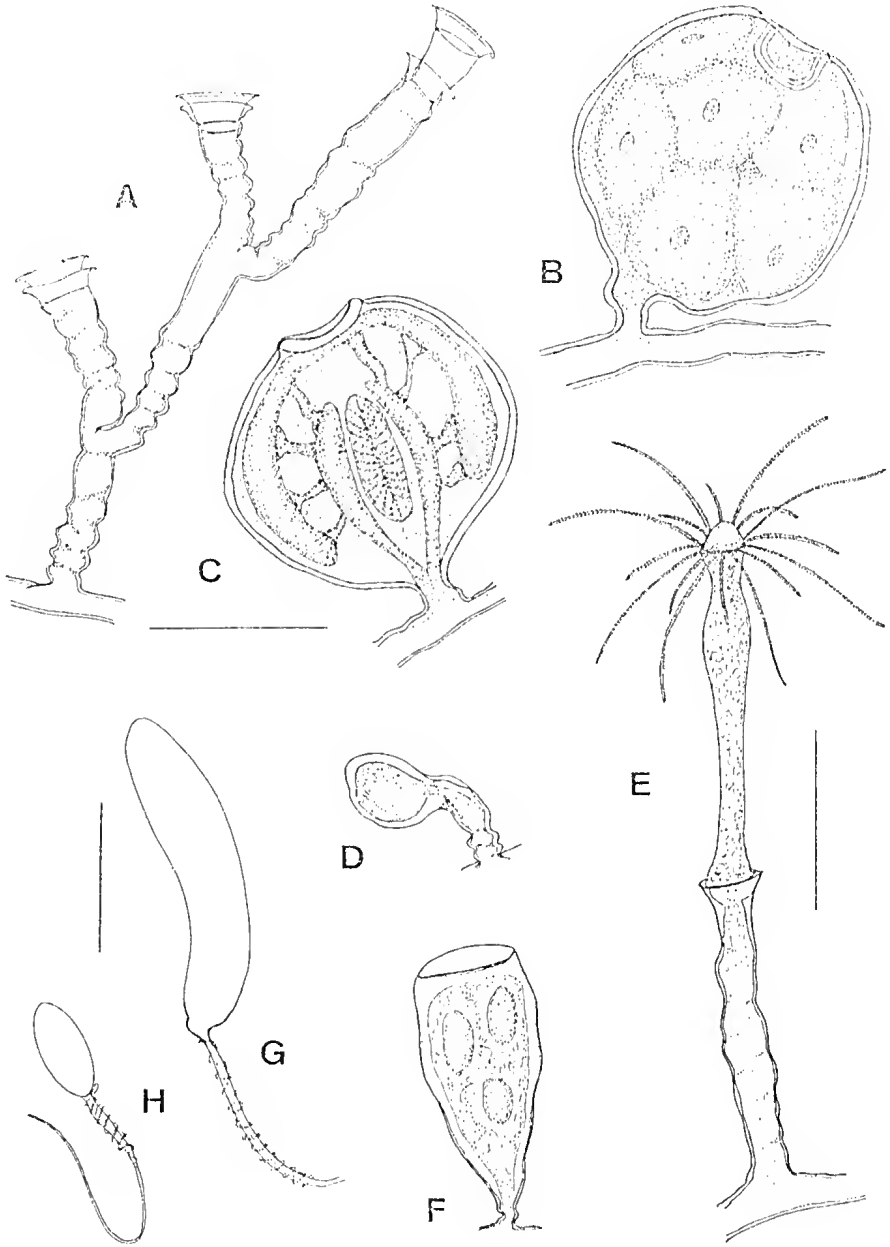
Fig. 1. A–D, *Halecium amphibolum* sp. nov. A, stem from holotype colony. B, female gonotheca with mature gonophore. C, nearly mature male gonophore. D, immature male gonophore. E–H, *Campalecium alcoicum* sp. nov. E, hydrophore with extended hydranth. F, gonotheca with nearly mature medusoid gonophores. G, micro-basic mastigophore from tentacles. H, oral microbasic mastigophore. Bar scales: A–D, 0.5 mm; E, 0.25 mm; G, H, 10 mm. F not drawn to scale.

examination of a large sample of fertile material revealed no evidence of a degenerate hydranth associated with the female gonophore such as occurs in *H. nanum*; the gonothecae are lenticular in shape with smooth perisarc, unlike the rugose gonothecae of *H. corrugatissimum*; and the aperture of the female gonotheca is a notch in the perisarc, not tubular as in *H. pusillum*.

Ecology. Halecium amphibolum sp. nov. is a seagrass obligate epiphyte (Watson 1992), found only at the type locality of Queenscliff in southeastern Australia. The colonies grow in the sheltered microhabitat of the axils of the seagrass leaves. They have a life-span of a few weeks from settlement to senescence and are fertile in spring.

Campalecium alcoicum sp. nov.

Fig. 1E–F

Type material. Holotype NMV F51789, a colony (alcohol preserved) on a bryozoan from wharf piles, 3 m, Point Henry, Port Phillip Bay, Victoria, coll. J. E. Watson, 11 Jan. 1992.

Description. Colony stolonal, many hydrophores arising from tubular hydrorhiza 0.04–0.06 mm in width. Hydrophores tubular, to 0.3–0.4 mm high, of same diameter as hydrorhiza, distal end expanded into shallow dish-shaped hydrotheca 0.01 mm deep and 0.04–0.07 mm wide at margin. A ring of desmocytes present.

Fully extended hydranth at least twice as high as hydrophore, column thin, thickening a little below origin of tentacles. Hypostome conical, surrounded by single, amphicoronate whorl of 18–20 fine, filiform tentacles.

Nematocysts small microbasic mastigophores, capsule 6–7 µm × 2µm, shaft about same length as capsule, thread very long (to 500 µm), numerous on tentacles; a few larger microbasic mastigophores around hypostome, capsule banana-shaped, 20 × 4 µm, shaft very thick and ropy, about 35 µm long, thread a little thinner, at least twice length of shaft.

Gonotheca arising from base of hydrophore and larger than it, top-shaped, widening distally to truncated summit, walls smooth, perisarc thin, containing three medusa buds at different stages of development.

Colonies transparent to white. Each medusa bud with a yellow spot.

Remarks. The bryozoan substrate of *Campalecium alcoicum* sp. nov. was on the mussel *Mytilus edulis planulatus* (Lamarck) growing on wharf pilings in sheltered water. The single

gonotheca found on the colony was damaged before measurements could be made.

Campalecium is best known from one widely distributed species, *C. medusiferum* Torrey, 1902. The hydroid phase of *C. medusiferum* has been recorded from the Mediterranean Sea, the Indo-West Pacific Ocean and the California coast, and the medusa has been recorded from the Mediterranean Sea, the tropical Atlantic Ocean and Malaysia.

Millard & Bouillon (1975) reported fertile colonies (without liberated medusae) of *Campalecium cirratum* (= *Eucheilota cirrata* Haeckel, 1879) from the Seychelles and included *C. medusiferum* in its synonymy. Boero (1981), however, doubted that these species are conspecific because: (i) the newly liberated medusa of *C. medusiferum* is different from that of *C. cirratum*; and (ii) the cnidome of the Seychelles species differs from that of *C. medusiferum*, the former containing microbasic mastigophores and "several other types of nematocyst in the tentacles" (Millard & Bouillon 1975: 8) while the latter has both macrobasic and microbasic mastigophores. He thus considered the Seychelles specimens probably to represent a new species.

Campalecium alcoicum is not closely related to either *C. medusiferum* or *C. cirratum?*, the differences being: (i) the larger hydrocaulus and the several kinds of tentacular nematocysts in the Seychelles species, compared with two kinds both of smaller size in *C. alcoicum*; (ii) the oral macrobasic mastigophores of *C. medusiferum* (see Boero 1981, fig. 5) were not found in *A. alcoicum*; and (iii) the absence of an intertentacular web from *C. alcoicum*.

The finding of microbasic mastigophores in *C. medusiferum* would bring the apparent relationship between this species and *C. alcoicum* much closer. Examination of living material revealed no trace of an intertacular web. If present, it is so reduced as to be vestigial. Since an intertentacular web is diagnostic of *Campalecium*, its absence from the Australian species suggests that the concept of the genus needs to be revised to accommodate varied development of this structure.

REFERENCES

ALDER, J., 1859. Description of three new sertularian zoophytes. *Annals and Magazine of Natural History, Series 3* 3: 353–355, pls 12–14.
BOERO, F., 1981. Systematics and ecology of the hydroid population of two *Posidonia oceanica*

meadows. *Pubblicazioni della Stazione zoologica di Napoli (Marine Ecology)* 2: 181–197.

BOUILLON, J., 1985. Essai de classification des Hydropolypes–Hydroméduses (Hydrozoa–Cnidaria). *Indo-Malayan Zoology* 1: 29–243.

HAECKEL, E., 1879. *Das System der Medusen. Erstes Teil einer Monographie der Medusen.* Jena, 360 p.

MILLARD, N. A. H., & BOUILLON, J., 1975. Additional hydroids from the Seychelles. *Annals of the South African Museum* 69: 1–15.

TORREY, H. B., 1902. Hydroids of the Pacific coast of North America, with special reference to the collection of the University of California. *University of California Publications, Zoology* 1: 1–104.

TREBILCOCK, R. E., 1928. Notes on New Zealand Hydroida. *Proceedings of the Royal Society of Victoria* 41: 1–31.

SARS, M., 1857. Bidrag til Kundskaben om Middelhavets Littoral-Fauna, Reisebemaerkninger fra Italien. *Nyt Magasin fr Naturvidenskaberne* 9: 110–164.

WATSON, J. E., 1992. The hydroid community of *Amphibolis* seagrasses in south-eastern and south-western Australia. *Scientia Marina* 52: 217–227.

CHITINOZOAN ASSEMBLAGES FROM THE PRAGIAN (LOWER DEVONIAN) OF EASTERN AUSTRALIA

Theresa Winchester-Seeto

Centre for Ecostratigraphy and Palaeobiology, School of Earth Sciences, Macquarie University, New South Wales 2109

Winchester-Seeto, T., 1993:11:01. Chitinozoan assemblages from the Pragian (Lower Devonian) of eastern Australia. *Proceedings of the Royal Society of Victoria* 105 (2): 85–112. ISSN 0035-9211.

Two Pragian sections from seven eastern Australian successions investigated have yielded chitinozoans; they are the Martins Well Limestone Member of the Shield Creek Formation, north Queensland, and the Coopers Creek Formation at Boola Quarry, Victoria. Chitinozoa from these sections are documented and the new species *Gotlandochitina kutjala* and *Angochitina cactula* are described. Comparison of the assemblages recovered in this study with those of contemporaneous faunas from other areas of Australia (Garra Limestone), Europe and north Africa demonstrate the facility of chitinozoans for intercontinental correlation. *Angochitina comosa* Taugourdeau & Jekhowsky, a well-known early Pragian chitinozoan, was recovered from the Martins Well limestone, verifying the position of the Lochkovian–Pragian boundary as previously determined from conodont evidence, and establishing the importance of the species as a reliable index in Australia, as it is also in south-western and central Europe and north Africa. *Angochitina caeciliae* Paris and *Bulbochitina bulbosa* Paris occur in strata of similar age in Australia and south-western Europe. As in Europe, strata of late Pragian age in eastern Australia yield few chitinozoans, pointing to a world-wide trend of reduced chitinozoan diversity in this interval. Marine regressions and a reduced number of suitable environments for preservation of chitinozoans are possible reasons for this phenomenon. A number of diagnostic assemblages based on zone fossils from Europe can be recognised in Australian successions. These are an *Angochitina comosa* assemblage from near the Lochkovian–Pragian boundary, succeeded by an *Angochitina caeciliae* assemblage, still within the *sulcatus* conodont Biozone, and a *Bulbochitina bulbosa* assemblage from the *kindlei* conodont Biozone.

PRAGIAN chitinozoans have been studied from only a small number of localities, primarily from north Africa and south-western and central Europe, thus concentrating the data in a limited palaeogeographic range. Although chitinozoans have proven their utility as biostratigraphic tools in these areas, the lack of more widespread data has skewed our knowledge of this time interval, leaving a number of unanswered questions; these include doubts as to whether chitinozoan biozonations developed in Europe can be used in an Australian context, and the allied problem of how useful chitinozoans are for intercontinental correlation. Our knowledge is further restricted by the fact that there is only scanty information on the upper Pragian, most studies having examined material only from near the Lochkovian–Pragian boundary. The present investigation, in tandem with a recent study of chitinozoans across the Lochkovian–Pragian boundary in the Garra Limestone of central New South Wales (Winchester-Seeto 1993), seeks to address some of these issues.

The first studies of Early Devonian chitinozoans were concentrated in north Africa in re-

sponse to the search for oil in the 1960s and 1970s. These studies included work on the Algerian Sahara (Taugourdeau & Jekhowsky 1960, Magloire 1967, Jardiné & Yapaudjan 1968), Libya (Massa & Moreau-Benoit 1976), Morocco (Rahmani 1978) and Tunisia (Grignani 1967). It is difficult to integrate this work fully with later investigations for two reasons. Firstly, these studies relied solely on illustrations from light microscopy, producing only silhouettes to document the fauna. It has since been demonstrated by Paris (1978, 1981a) that observations of opaque chitinozoans by light microscopy may omit important specific and generic characters, such as ornamentation, and may lead to misidentification of taxa (Paris 1978: 195). Consequently, comparisons between faunas illustrated solely as silhouettes and those depicted by scanning micrographs are unreliable. Secondly, the stratigraphic control on the original cores and sections used in these early studies may be based either on very limited information from other fossils or, in some cases, on outdated interpretations, thus requiring some revision. Paris (1981a: 357) attempted to

align the assemblages found by Taugourdeau &
Jekhowsky (1960) and Magloire (1967) based on
the chitinozoan zonation erected in France; this
reinterpretation has been adopted in the present
study.

Other studies on Pragian chitinozoans have
included those from south-western Europe
(France: Paris 1976, 1980, 1981a; Spain: Diez &
Cramer 1978), central Europe (Poland: Wrona
1980; Bohemia: Chlupáč et al. 1985) and China
(Gao 1986). The time parameters for the last
study are not specifie and only a pre-*dehiscens*
age is given; the composition of the fauna, how-
ever, suggests a Pragian age. Paris (1981a)
suggested amendments to the stratigraphie
alignments for the Spanish study, and these have
been adopted for the purposes of this inves-
tigation. The works of Diez & Cramer and of
Gao use only silhouettes for identification, and
thus their results must be treated with some
caution.

The aims of the present study were:
1. To document chitinozoan faunas from the
Pragian of eastern Australia.
2. To compare these faunal assemblages with
studies of contemporaneous strata elsewhere in
Australia and globally.
3. To evaluate the intercontinental utility of
species used as index fossils in Europe.
4. To develop a preliminary zonation for eastern
Australia.

METHODS

Seven sequences from eastern Australia, cover-
ing the entire Pragian interval, were investigated
for this study (Figs 1, 2). The main criterion for
selection of the limestone strata was that a firm
biostratigraphie framework, based on conodont
data, was already in place (e.g. Mawson et al.
1988, 1992; Wilson 1989). In order to achieve
the greatest precision in correlating chitinozoan
data with results obtained from conodont work,
concurrent   collections   of   conodont   and
chitinozoan samples were made from surface
outcrops.

Methods of processing for chitinozoans fol-
lowed those outlined by Paris (1981a), including
initial treatment of 50 g of crushed rock with
10% HCl until all the carbonate had been dis-
solved, followed by acid digestion by 70% HF for
12–48 hours. Nitric acid (concentrated) was
used when necessary for surface etching,
dissolving of fluorite salts and destruction of
amorphous organic matter. The residue was
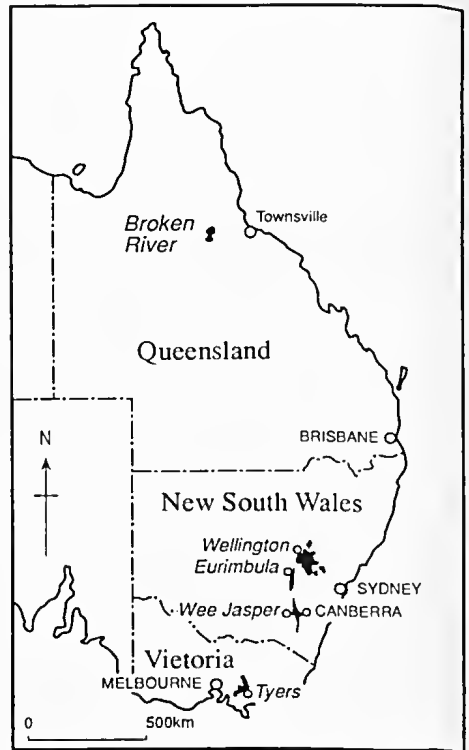
Fig. 1. Map of eastern Australia showing Lower
Devonian strata investigated for this report.

then separated through a 53 µm sieve and picked
with a micropipette. Representatives of each
species, especially well-preserved specimens,
were selected and mounted on glass coverslips
for examination with a scanning electron micro-
scope, as described by Paris (1981a).

SEQUENCES INVESTIGATED

Only two of the seven sequences investigated
yielded well preserved chitinozoans in sufficient
numbers to prove useful for such a biostrati-
graphie study. No chitinozoans were recovered
from a section through the Garra Limestone
near Eurimbla (EUR), central New South Wales,
spanning the time interval from *delta* to *sulcatus*
conodont Biozones (Sorentino 1989). A second
section through the Garra Limestone near
Mountain View homestead (MVR) yielded only
three badly deteriorated, unrecognisable speci-
mens; this section was documented by Wilson
(1989) who suggested that the section probably
included the *pireneae* conodont Biozone. A
section through the Arch Creek Limestone

SYSTEM	STAGE	CONODONT ZONE	
LOWER DEVONIAN	EMSIAN	perbonus	
		dehiscens	
	PRAGIAN	pireneae	
		kindlei	
		sulcatus	
	LOCHKOVIAN	pesavis	
		delta	
		eurekaensis	
		woschmidti	

■ Abundant chitinozoans

◨ Few chitinozoans

□ No chitinozoans

Fig. 2. Stratigraphic ranges of Lower Devonian sequences investigated for this report. For detailed stratigraphic information see Mawson et al. (1988, 1992), Mawson & Talent (in press) and Wilson (1989).

member of the Shield Creek Formation, northern Queensland, spanning the *pesavis–sulcatus* conodont Biozones (Bear & Benson in Mawson et al. 1988) gave no results. The TANK section through the lower part of the Cunningham Formation (Talent & Mawson, in prep.), central New South Wales, and the CABL section of the Cavan Bluff Limestone at Wee Jasper, southern New South Wales (Mawson et al. 1992), covering the Pragian–Emsian boundary, were likewise barren of chitinozoans (see Figs 1, 2).

More promising results were obtained from a section through the Martins Well Limestone Member of the Shield Creek Formation in the Broken River area of northern Queensland. A small but nonetheless significant yield was also obtained from a measured section at Boola Quarry near Tyers, eastern Victoria.

The Martins Well Limestone Member has been thoroughly documented by Jell (1968), Telford (1975), Wyatt & Jell (1980) and, more recently, by Mawson et al. (1988). The limestone is a bioclastic calcarenite interpreted as representing a 'shallow marine deposition on a broad, stable shelf' (Wyatt & Jell 1980: 202), probably at the start of a marine transgression. The 120 m section (Fig. 3) measured through this limestone is the same as that sampled for the conodont work carried out by Benson & Bear (in Mawson et al. 1988) and repeats one of the studies by Telford (1975).
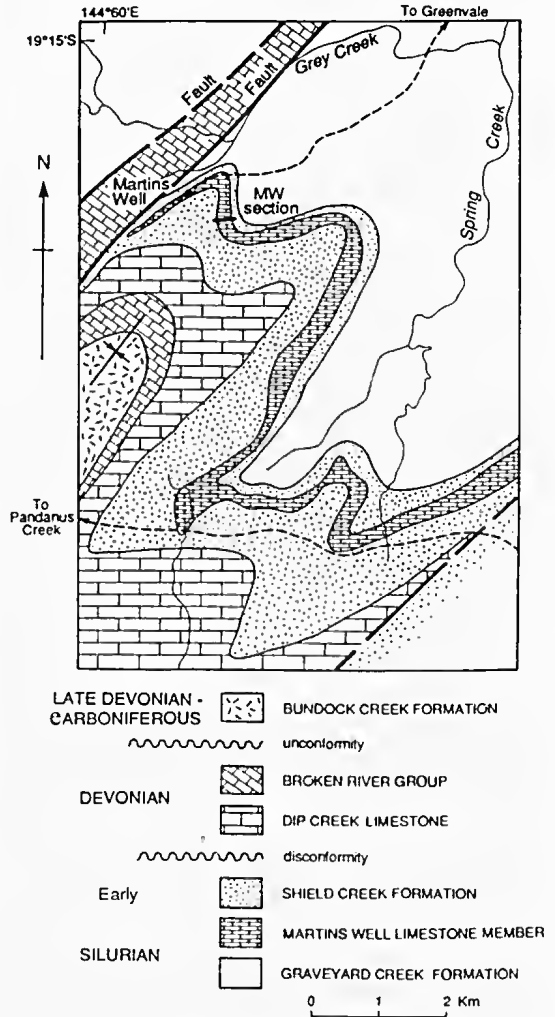

Fig. 3. The Broken River area of northern Queensland, showing the location of the Martins Well section (prefix MW); after Telford (1975).
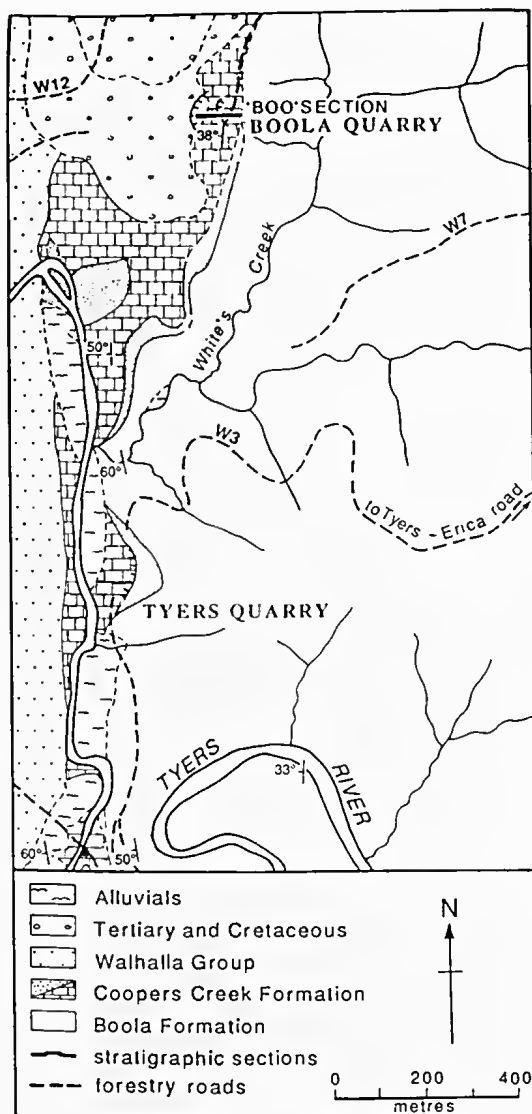
Fig. 4. The Coopers Creek Formation, showing the location of the section through Boola Quarry (prefix BOO); based on a map surveyed by Kenney (1937).

Boola Quarry is situated within the Tyers Limestone Member of the Coopers Creek Limestone. (Fig. 4). The limestone is generally richly fossiliferous, with faunas of corals and conodonts that were described by Philip (1962, 1965) and Philip & Pedder (1967). VandenBerg (1988: 122) suggested that the limestone represents a relatively shallow water deposit, with an unresolved question as to whether the strata are *in situ* or are the result of a mass-flow event.

Rehfisch & Webb (1993) reinterpreted the unit as a carbonate fan deposited in deep water, with possible reworking. The age of the strata has been unclear, but recent work by Mawson & Talent (in press) shows that, while the base of the Boola Quarry section is of *sulcatus* Biozone age, this zone is replaced low in the section by the *kindlei* Biozone, 7.1 m above the base of the Coopers Creek Limestone.

CHITINOZOAN DATA

Chitinozoan yields from the Martins Well Limestone are low to average, with fossils recovered in 18 out of 29 samples and ranging in abundance from 0.02 to 4 specimens per gram of limestone. The fauna is relatively well-preserved, amber to black in colour, with most individuals in full relief or only partially flattened. Breakages are common but some ornamentation is preserved on most specimens. Many chitinozoans display circular 'holes' resembling those figured by Laufeld (1974: 118) and which are interpreted as traces of parasites. These holes may have been partially responsible for the breakages by weakening the vesicle wall.

The chitinozoans from Martins Well tend to occur in beds either with no macrofossils or where these are only small in size. Small crinoid stems are commonly found in the same beds (e.g. bed numbers MW 13.7, 15.0, 18.6, 20.9, 25.4 rare, 34, 34.2, 39.9, 49.0, 51.0, 69, 74, 78.6, 95.6), but in some places crinoid calices, corals, bryozoans, small brachiopods, small gastropods and, more rarely, stromatoporoids occur together with the chitinozoans. The macrofossil assemblage suggests an extremely shallow depositional environment, and the presence of crinoid calices suggests a relatively quiet water regime. The microfauna consists of scolecodonts, conodonts and the linings of agglutinated microforaminiferans.

In contrast, Boola Quarry yielded very few chitinozoans or other microfauna, apart from conodonts which are relatively abundant. In the 20 m section in the lower part of Boola Quarry, commencing from the base of the Coopers Creek Limestone, only 4 beds out of 24 contained any trace of chitinozoans and only one bed produced more than 10 individuals. All chitinozoans recovered show a high degree of organic maturation; thin-walled genera are scarce, and those that do occur are represented by badly broken specimens with deteriorated surfaces having

little or no ornament. There are, however, some reasonably well-preserved specimens of thick-walled genera, e.g. *Bursachitina* and *Bulbochitina*, in full relief and with ornamentation more or less intact. The varied nature of the preservation suggests that conditions were not ideal for the conservation of these fossils and only robust groups were preserved. Few macrofossils were observed in the section and the microfauna is relatively sparse, consisting of rare scolecodonts and microforaminiferal linings, a few agglutinated foraminiferal tests and conodonts.

STRATIGRAPHIC DISTRIBUTION OF CHITINOZOA

Martins Well Limestone

The Martins Well fauna is dominated by four species, *Angochitina* sp. B, *Angochitina comosa* Taugourdeau & Jekhowsky, *Angochitina dimorpha* Taugourdeau & Jekhowsky and *Gotlandochitina kutjala* n. sp.; together these make up 53% of the population (Fig. 5; Table 1).

The results of the Martins Well study show a number of similarities with a previous investigation of a section through the Garra Limestone, spanning the Lochkovian–Pragian boundary (Winchester-Seeto 1993). Chitinozoans from the GCR (Golf Course) section of the Garra Limestone were assigned to three assemblages. Assemblage 1, from the top of the *pesavis* conodont Biozone, was characterised by the presence of *Angochitina hypenetes* Winchester-Seeto and also contained *Calpichitina gregaria*? Paris, *Muscochitina*? sp. and *Calpichitina velata* (Wrona). The succeeding Assemblage 2, located stratigraphically just above the Lochkovian–Pragian boundary (i.e. just into the *sulcatus* conodont Biozone), was defined by the occurrence of *Angochitina comosa* Taugourdeau & Jekhowsky and also included *Muscochitina*? sp. and *Calpichitina velata*. Assemblage 3, still within the *sulcatus* conodont Biozone, contained *Angochitina caeciliae* Paris, *Gotlandochitina* sp. C, *Bursachitina mawsonae* Winchester-Seeto, *Angochitina* aff. *A. crassispina* Eisenack, *Angochitina* cf. *A. callawayensis* Urban & Kline and *Gotlandochitina* aff. *G. ramosus* (Paris).

Five species from the Martins Well section were also found to occur in the lower Pragian segment of the GCR section: *Angochitina comosa*, *A. hypenetes*, *Bursachitina mawsonae*, *Angochitina* cf. *A. callawayensis* and *Ango-*

chitina aff. *A. crassispina*. The first three of these species occur in Assemblage 2 of the Garra Limestone. The presence of *A. comosa* very low in the section from the Martins Well Limestone indicates a close correlation with Assemblage 2 of the Garra Limestone, and thus a very early Pragian age (i.e. *sulcatus* conodont Biozone).

Benson & Bear (in Mawson et al. 1988) showed the base of the Martins Well Limestone to lie in the *pesavis* conodont Biozone, based on the occurrence of *Icriodus steinachensis* 8.5 m above the base of the section. They also suggested that the *pesavis* Biozone was represented much higher in the section by elements they refered to *Pedavis pesavis*? (Mawson et al. 1988, table 7). However, as these elements do not include an I element their assumption may be suspect. Further, the specimen they identified as *Kimognathus alexeii* has been re-examined and found to be a damaged specimen of a species of *Pedavis* (R. Mawson pers. comm.), casting doubt on the age of the upper part of the section. In his section No. 3658, parallel to the section from which Benson & Bear's samples were collected, Telford (1972, 1975) recovered two specimens of *Eognathodus sulcatus sulcatus* at 9 m and 10.5 m above the base of the section (Telford 1975, pl. 12, figs 5–7). With the incoming of *E. sulcatus* at this level it appears that the Lochkovian–Pragian boundary is fairly tightly constrained somewhere between 8.5 m and 9 m above the base of the Martins Well Limestone Member. This is corroborated by the presence of *Angochitina comosa* amongst the first yielding samples of the section used in the present study (i.e. sample MW 18.6, 24.6 m above the base of the section).

The absence of *Angochitina caeciliae* and *Gotlandochitina* aff. *G. ramosus* in the Martins Well material suggests that this section does not extend as high as Assemblage 3 of the Garra Limestone, despite the presence of *Angochitina* cf. *A. callawayensis* and *A.* aff. *A. crassispina* at Martins Well. Two species, previously known only from the Lochkovian in Australia, are now found to extend into the Pragian; i.e. *Gotlandochitina implicationis* (Urban) and *Angochitina* sp. A (formerly *Angochitina* sp. B of Winchester-Seeto 1993).

A number of key species also occur in faunas from overseas. *Angochitina comosa* has been found in the lower Pragian in north Africa (Taugourdeau & Jekhowsky 1960, Grignani 1967, Magloire 1967, Rahmani 1978), in Spain (Diez & Cramer 1978), in France (Paris 1976), in Bohemia (Chlupáč et al. 1985) and in China
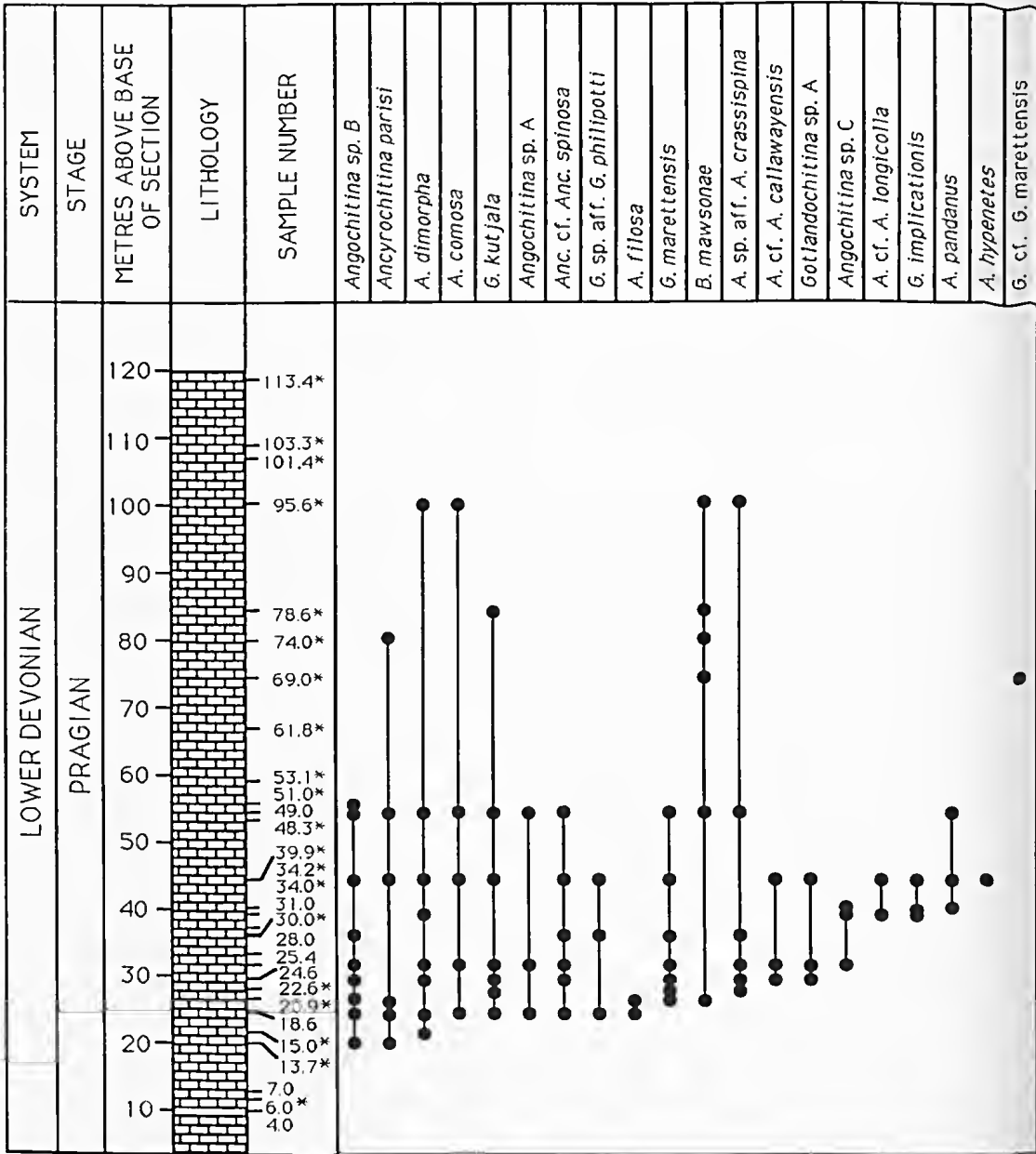
Fig. 5. Stratigraphic ranges of Chitinozoa in the Martins Well section (MW) of the Martins Well Limestone Member, Shield Creek Formation, Broken River area of northern Queensland; * indicates beds yielding conodonts.

(Gao 1986). Paris (1981a) used this species, along with *Margachitina catenaria tenuipes* Paris, to define his Zone 32, found just above the Lochkovian–Pragian boundary. *Angochitina dimorpha* was also found in the lower Pragian of north Africa (Taugourdeau & Jekhowsky 1960),

and *Angochitina cactula* n. sp. (= *Angochitina* cf. *A. crassispina* Eisenack of Wrona 1980) was found in the lower Pragian of Poland.

Slight differences exist in the stratigraphic position of some species. For instance, *Angochitina* cf. *A. callawayensis* was found slightly

Table 1. Distribution and abundance of chitinozoans from the Martins Well section (MW) of the Martins Well Limestone Member, Shield Creek Formation, and from the Boola section (BOO) of the Tyers Limestone Member, Coopers Creek Formation.

Sample Number	MW 13.7	15	18.6	20.9	22.6	24.6	25.4	30	34	34.2	39.9	49	51	69	74	78.6	95.6	BOO 13.1	17.8	28
Meters above base of section	19.7	21	24.6	26.9	28.6	30	31.4	36	40	40.2	45.9	55	57	75	80	84.6	102	13.1	17.8	28
Anc. sp. aff. A. parisi	1		17																	1
Angochitina sp. B	1		28	1		18	21	2			2	2								
A. dimorpha		1	20	1		12	34		1		18	11	1		1		1			
A. comosa			22				43				13	5					2			
Angochitina			3				2				3	4								
G. sp. aff. G. philpotti			12									2		1		1				
G. kulata			31	1	1	24	31	2			8									
Anc. spinosa var. gibba					1	5	8	1			24	9		1			3			
G. marettensis				1	1	11	15	2			2	1		2	1	2				
B. mawsonae				2	1					8	21	3								
A. sp. aff. A. crassispina					1	7	4	1				3								
Gotlandochitina						6	1		1			3					2			
A. cf. A. callawayensis						5	6				2									
Angochitina sp. C							26				12									
Angochitina sp. E														1						
G. implicationis										5	2	13								
A. cactula									4	2	1									
A. hypenetes											1									
G. cf. G. marettensis												3								
Sp. indet			17		2		10	2			13	8								
B. bulbosa																		22	3	
Bursachitina																		5	2	
Gotlandochitina																				

higher stratigraphically by Paris (1976) in Saint-Céneré. *Ancyrochitina spinosa gibba* n. var. has previously been cited only from the Middle Devonian (Urban & Kline 1970), but this taxon appears to be merely a morphological variant of *A. spinosa* Eisenack, which ranges from the Silurian to the Middle Devonian. Similarly, *Gotlandochitina marettensis* Paris has only previously

been found in the Emsian (Paris 1981a, 1981b), though there is a possible evolutionary relationship between this species and *Angochitina bifurcata* Collinson & Schwalb, found in the Lochkovian. This would account for its presence in the Pragian of Australia.

Several important species, common in coeval deposits across the world, are missing from Australian strata so far studied: *Fungochitina pistilliformis lata* (Taugourdeau & Jekhowsky), *Angochitina devonica* Eisenack and *Cingulochitina serrata* Taugourdeau & Jekhowsky from south-western Europe and north Africa; *Urochitina simplex* Taugourdeau & Jekhowsky from north Africa; *Armoricochitina ceneratiensis* (Paris) from south-western Europe; *Margachitina caternaria tenuipes* Paris from south-western and central Europe as well as north Africa; and *Ancyrochitina ancyrea* (Eisenack) and *Ancyrochitina tomentosa* Taugourdeau & Jekhowsky from central Europe and north Africa. The reasons for the absence of these species in Australia is unknown, but it is interesting to note that four of the genera—*Urochitina, Cingulochitina, Armoricochitina* and *Margachitina*—have not yet been found in any Australian deposit, nor were they reported in the Chinese fauna documented by Gao (1986).

Boola Quarry

Only four species were recovered from the section at Boola Quarry: *Bulbochitina bulbosa* Paris, *Gotlandochitina* sp. B, *Bursachitina* sp. and *Angochitina* sp. D (Table 1). *Gotlandochitina* sp. B was also found in Assemblage 3 of the Garra Limestone; this assemblage occurred directly above that containing *Angochitina comosa*.

Bulbochitina bulbosa was used by Paris (1981a: 379) to define his Zone 36 for south-western Europe; this zone occurs in the middle Pragian, within the *kindlei* conodont Biozone. *B. bulbosa* occurs only in two samples from Boola Quarry: sample BOO 13.1, approximately 6 m above the *sulcatus–kindlei* boundary which is 7.1 m above the base of the section (Mawson & Talent in press); and sample BOO 17.8, 11 m above the boundary. The occurrence of *B. bulbosa* in Australia is thus stratigraphically very close to but slightly lower than its occurrence in Europe.

PROBLEMS IN THE PRAGIAN

Chitinozoans have been recovered from Pragian strata in only three sections in Australia, two

from near the boundary of the *pesavis–sulcatus* conodont biozones and one spanning the *sulcatus–kindlei* boundary. Despite repeated attempts in a number of other Pragian limestone successions (representing a range of different environments) no other strata yielded chitinozoans. Approximately 100 samples from six sections spanning the *kindlei* and *pireneae* conodont biozones in eastern Australia were processed for chitinozoans; only seven of these samples yielded chitinozoans and only four produced specimens that were well enough preserved to identify, the latter being from Boola Quarry (Winchester-Seeto unpub. data).

This stratigraphic interval, covering the upper *sulcatus* to the lowermost *dehiscens* conodont biozones (i.e. middle Pragian to just above the Pragian–Emsian boundary), is documented in only four studies world-wide (Paris 1981a, 1981b; Massa & Moreau-Benoit 1976; Diez & Cramer 1978). The small number of investigations may indicate a lack of interest in this interval or reflect unsuccessful attempts to find chitinozoans. The latter is certainly true for Australia, as exemplified by the difficulties encountered in finding suitable localities where chitinozoans can be recovered. Unpublished studies from Europe and north Africa suggest, however, that at least in the northern hemisphere the problem may be related to insufficient exploration (Paris pers. comm. 1992).

Where chitinozoans have been recovered from the middle and upper Pragian, it is apparent that their abundance in this interval is much lower than in other parts of the Lower Devonian and that species diversity is also reduced. Similar patterns have been observed by some researchers on conodonts; for example, Sweet (1985: 490) presented a graph showing that the species diversity of conodonts from the Upper Cambrian to the top of the Lower Devonian reaches a peak near the Lochkovian–Pragian boundary and drops dramatically to a low near the middle of the Pragian, before rising slightly at the Pragian–Emsian boundary. Bayer & McGhee (1989: 7) presented a similar plot, with a decrease in species diversity appearing slightly higher in the Pragian (Siegenian) and continuing well into the Emsian (the differences in timing of these events may be an artefact of the sampling and graphical procedures used by the different workers). Other researchers found that the drop in conodont species diversity occurs much lower stratigraphically and thus precedes that shown by chitinozoans. Ziegler & Lane (1987: 153) noted a decrease in conodont species diversity in

the uppermost *pesavis* conodont Biozone, followed by a prolonged interval of low diversity until very high in the Pragian. Data from the Garra Limestone also showed a drop in conodont species diversity high in the upper Lochkovian *pesavis* Biozone (Talent et al. in press).

Although the exact timing is difficult to assess, given the data available, there appears to be a widespread or global event occurring in the Pragian, affecting both conodonts and chitinozoans (and perhaps other microfauna and macrofauna). The reason for such a drop in diversity is unclear, but in the *kindlei–pireneae* interval (when chitinozoan abundance and diversity is lowest) a marine regression has been postulated for Australia (Talent & Yolkin 1987).

As a number of chitinozoan species (e.g. *Angochitina dimorpha* Taugourdeau & Jekhowsky, *Ancyrochitina parisi* Volkheimer, Melendi & Salas and *Sphaerochitina nodulosa hispida* Taugourdeau & Jekhowsky) occur before and after but not within this interval, an extinction event is not indicated. Added to this is the observation that genera with thin-walled vesicles (such as *Angochitina* or *Gotlandochitina*) are under-represented in the middle and upper Pragian, or are frequently so poorly preserved as to be unidentifiable at the species level (e.g. Boola Quarry, this study; Paris 1981a: 342). Recently, Paris (pers. comm. 1992) recovered representatives of thin-walled forms from well-preserved material from north Africa, but this limited occurrence underlines the comparative rarity of pristine preservation conditions in this stratigraphic interval.

These observations suggest that the drop in species diversity may be connected with preservation of the fossils, rather than a real gap in their temporal distribution. It has long been believed that chitinozoan vesicles do not survive in highly oxidised environments because the organic test is rapidly decomposed (e.g. Laufeld 1974, Paris 1981a). Perhaps the reduced number of chitinozoans in this stratigraphic interval can be explained by a decrease in the number of environments suitable for the preservation of the fauna, i.e. dysaerobic environments. Our understanding of the causes of low oxygen environments is limited and includes models ranging from stratified basins, based on salinity or thermal differences, upwelling, expansion or contraction of the oxygen minimum zone, and the effect of sea level and/or bottom topography (Tyson & Pearson 1991). A change in any one of these factors, or perhaps a combination of them,

may have led to a reduetion in suitable preservation sites for organie microfossils.

More work is needed to establish whether the paueity of data for this interval represents a real gap in the geographic and/or temporal distribution of chitinozoans or is an artefact of sampling. Further study is also required to verify the apparent decrease in numbers of thin-walled genera.

PRELIMINARY CHITINOZOAN BIOZONATION FOR EASTERN AUSTRALIA

The only recent attempt to erect a ehitinozoan biozonation for the Devonian was by Paris (1981a) for south-western Europe. There are a number of similarities between the assemblages found there and in Australia, and a number of

SYSTEM	STAGE	CONODONT ZONE	CHITINOZOAN BIOZONES OF AUSTRALIA (PRELIMINARY)	CHITINOZOAN BIOZONES OF S.W. EUROPE (PARIS, 1980)
LOWER DEVONIAN	EMSIAN	dehiscens		37 Burs. riclonensis/ Bulb. bulbosa
				36
	PRAGIAN	pirenae		Bulb. bulbosa
			NO YIELDS AT THIS TIME	
		kindlei		35
				Burs. maritima
		sulcatus	Bulb. bulbosa ?— — — — — ? ?— — — — —? A caeciliae	34 G. jouannensis/ A. caeciliae
			A. comosa	33 M. catenaria tenuipes 32 A. comosa/ M. catenaria tenuipes

Fig. 6. Preliminary chitinozoan biozonation of the lower Pragian in castern Australia, and a comparison with the biozonation erected by Paris (1981a) for south-western Europe.

differences (Fig. 6). Zones 31 and 32 from Europe arc partially based on the presenee of *Margachitina catenaria tenuipes* Paris; however, *Margachitina* has not yet been found in Australia and is thus unavailable for stratigraphie use here. Zone 31 also contains *Angochitina comosa* Taugourdeau & Jekhowsky, found in a similar position (i.e. close to but slightly above the Lochkovian–Pragian boundary) in both the Garra Limestone and the Martins Well Limestone. In Australia, *A. comosa* is usually accompanied by *A. hypenetes* Winchcster-Secto and *Bursachitina mawsonae* Winehester-Secto. Thus the first diagnostic assemblage in Australia is characterised by the first oceurrence of *A. comosa.*

Work on the Garra Limestone demonstrated that the assemblage containing *A. comosa* was immediately followed by one containing *Angochitina caeciliae* Paris (Winchester-Seeto 1993). In Europe, Zones 31 and 32 are followed by a zone containing both *A. caeciliae* and *Gotlandochitina jouannensis* Paris; the latter has not yet been found in Australia. Based only on the Garra Limestone, so far, the next Australian assemblage could be defined by the first appearance of *A. caeciliae.* In the Garra Limestone this species was accompanied by *A. comosa, B. mawsonae* and *Gotlandochitina* cf. *G. ramosus* Paris.

Bursachitina maritima (Paris), used by Paris to define Zone 34 from Europe, has yet to be found in Australia. On the other hand, *Bulbochitina bulbosa* Paris, from Zone 36 near the top of the Pragian, has been found in Australia from the *kindlei* conodont Biozone.

Thus, based on the limited data from the three areas studied to date, it has been possible to recognise three distinctive and diagnostic assemblages from Pragian strata in Australia. That intracontinental eorrelation is possible is exemplified by the presenee of *Angochitina comosa* in the GCR seetion of the Garra Limestone and in the Martins Well section, the entry of the species in both sections being approximately eontemporaneous aeeording to conodont data. The same three assemblages, moreover, enable intereontinental eorrelation. *A. comosa,* for example, has been used in conjunction with the conodont *Eognathodus sulcatus sulcatus* Philip for definition of the Lochkovian–Pragian boundary at the global stratotype in Bohemia (Chlupáč & Oliver 1989) and can be used similarly in Australian strata. The *Angochitina caeciliae* assemblage occurs stratigraphically above *A. comosa* in south-western Europe, within the *sulcatus* conodont Biozone, as it does in Aus-

tralia, but without the intervening *Margachitina catenaria tenuipes* assemblage. *Bulbochitina bulbosa* is found within the *kindlei* conodont Biozone in Australia and in south-western Europe. Despite the slight anomalies between occurrences in Europe and Australia, the wide geographic spread and short stratigraphic time-span of the assemblages listed above make them useful additions to the biostratigraphic arsenal of Australian palaeontologists (see Fig. 6).

CONCLUSIONS

1. Chitinozoans have proved to be of biostratigraphic value in the lower Pragian of eastern Australia; diagnostic assemblages based on zone fossils from Europe can be recognised in Australian strata, facilitating subdivision of the *sulcatus* conodont Biozone.
2. The middle and upper Pragian of eastern Australia seems to be lacking deposits that yield abundant, well-preserved chitinozoans. This may be a worldwide phenomenon.
3. Three species in particular prove to have intercontinental utility in correlation, namely *Angochitina comosa* Taugourdeau & Jekhowsky, *A. caeciliae* Paris and *Bulbochitina bulbosa* Paris. Other species that may also be useful are *Angochitina dimorpha* Taugourdeau & Jekhowsky, *A. cactula* n. sp., *Ancyrochitina spinosa gibba* n. var. and *Gotlandochitina implicationis* (Urban).
4. Four genera (*Urochitina*, *Cingulochitina*, *Armoricochitina* and *Margachitina*) have so far not been recovered in Australia, suggesting that their distribution may be provincial or perhaps facies dependent.

SYSTEMATIC PALAEONTOLOGY

As there is no universally accepted suprageneric nomenclature for chitinozoans, the system used by Laufeld (1974) has been followed with the genera listed alphabetically. Abbreviations used for genera are: *Anc.* = *Ancyrochitina*, *A.* = *Angochitina*, *Bu.* = *Bulbochitina*, *B.* = *Bursachitina*, *G.* = *Gotlandochitina*.

All measurements are taken in microns (μm). Abbreviations used in the text are: L = length of vesicle; Lc = length of chamber; Ln = length of neck; Dmax = maximum diameter of chamber; Dn = diameter of neck; Da = diameter of aperture; Lsp = length of spines.

A correction factor of 0.7 has been used for those individuals whose diameter has been distorted by total flattening; this follows, in part, the precedent set by Jaglin (1986). Most of the specimens recovered in this study were in full relief or only partially flattened, so that this correction was applied infrequently.

Type and figured specimens are housed in the collections of the Queensland Museum, South Brisbane (numbers prefixed by QMF) and the Museum of Victoria, Melbourne (numbers prefixed by NMV P). Localities are designated as MW for samples from the section through the Martins Well Limestone and BOO for the section in Boola Quarry.

Morphological terms used in this paper are those defined by Laufeld (1974: 37–38) and by Paris (1981a: figs 56, 57).

Genus Ancyrochitina Eisenack, 1955

Type species. Conochitina ancyrea Eisenack, 1931.

Ancyrochitina aff. Anc. parisi Volkheimer, Melendi & Salas, 1986

Fig. 7F–I

Material. Twenty-four specimens from samples MW 18.6 and 49.

Measurements. Taken from six specimens from samples MW 18.6 and 49. L 146–172 (Av. 157.3); Lc 78–99 (Av. 89.5); Ln 54–81.6 (Av. 67.6); Dmax 54.4–64.3 (Av. 59.8); Dn 20.2–34 (Av. 27.2); Lsp max 13.6; L/Lc 1.6–2.0; L/Dmax 2.3–2.9.

Description. A species of *Ancyrochitina* with a cylindrical neck surmounting an ovoid to conical chamber. Flexure is indistinct, leading to a relatively long neck occupying one-third to one-half the total vesicle length. The base is convex but may be flat to weakly concave in compressed specimens.

Surface sculpture appears at the basal edge or on the neck, with occasional spine bases visible on the flanks. Basal processes are generally short and may be simple or bifurcate, in some instances with the distal ends joined. Ornamentation on the neck consists of relatively short, simple spines which spread up to the oral periphery.

Remarks. The specimens from Martins Well closely resemble *Ancyrochitina parisi* from Argentina but include some individuals with a more ovate chamber with maximum diameter about half-way along the length of the chamber, in addition to the more typical conical chamber shape of *Anc. parisi*. The Australian specimens are approximately half the size of those from Argentina, but the proportions of total length to
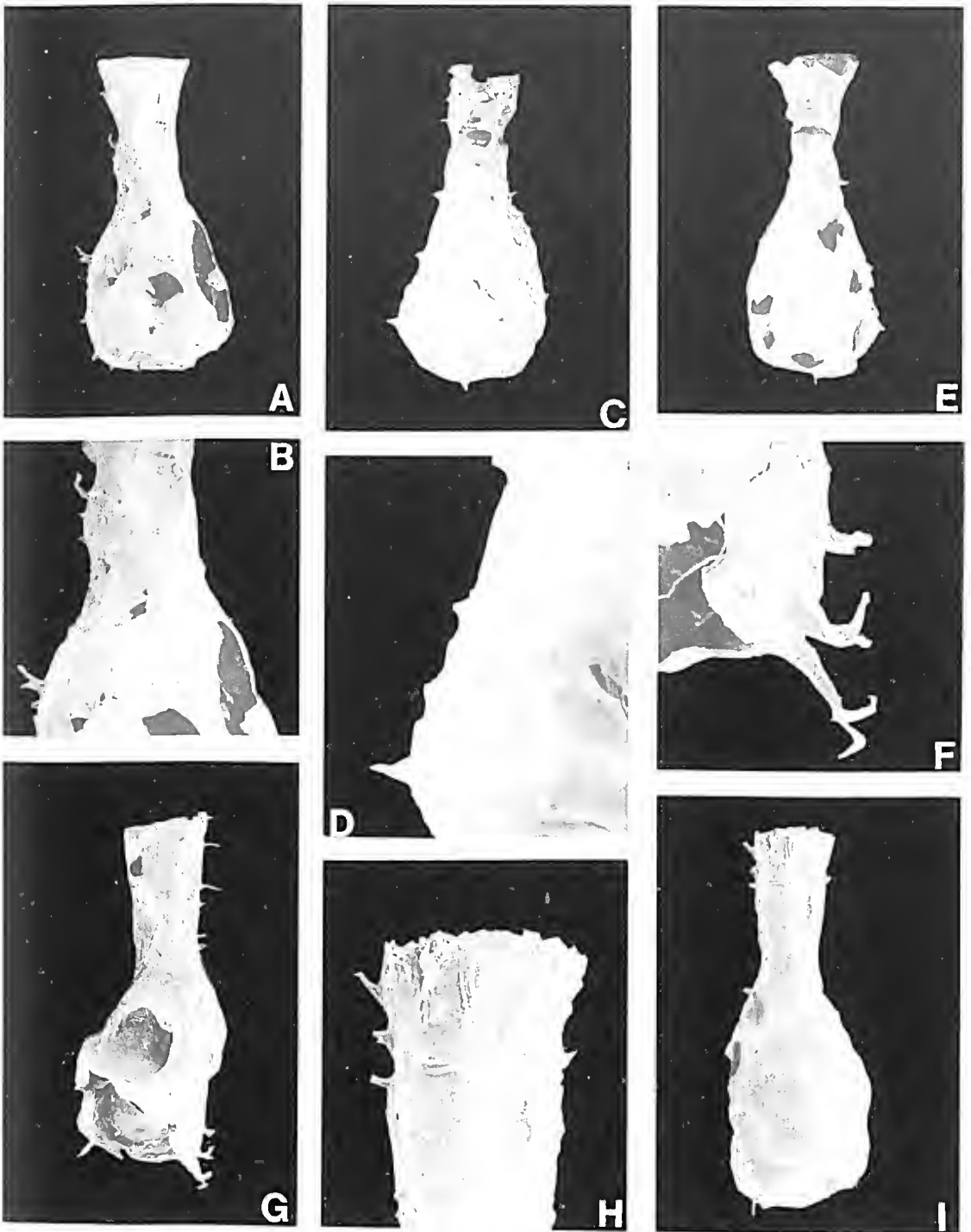
Fig. 7. A–E, *Angochitina* sp. B. A, B, QMF 25482, × 300, and enlargement of neck × 600, MW 39.9. C, D, QMF 25483, × 350, and enlargement of chamber showing unusual ornamentation × 900, MW 24.6. E, QMF 25484, × 350, MW 24.6. F–I, *Ancyrochitina* aff. *Anc. parisi* Volkheimer et al., MW 49. F, G, QMF 25485, enlargement of base of chamber showing appendices × 1300, and × 350. H, I, QMF 25486, enlargement of neck × 1000, and × 350.

length of body chamber, total length to maximum diameter, and length of ornamentation to total length are similar.

Sculptural elements are also very similar but in general, as is often the case in Australian material, they are much shorter; for example, *Anc.* aff. *Anc. parisi* has shorter basal processes and shorter spinose ornamentation on the neck. Basal processes are also much finer on *Anc.* aff. *Anc. parisi*. Rare examples can be found of specimens with distal processes joined by a membrane, both on the neck and on the basal edge; this parallels the occurrence noted by Volkheimer et al. (1986).

Additional, better preserved material of the Australian taxon may show it to be conspecific with *Anc. parisi*.

Ancyrochitina spinosa var. gibba n. var.

Fig. 8H

Ancyrochitina spinosa Eisenack 1959: 13–14, pl. 2, figs 1–2.
Ancyrochitina cf. *Anc. spinosa.*—Urban & Kline 1970: 71, pl. 18, figs 1–3, 14.

Etymology. Latin 'gibber' meaning swollen, referring to the shape of the neck.

Holotype. Urban & Kline (1970, pl. 18, fig. 1).

Type locality. Cedar City Formation, Whetstone Creek, north of Williamsburg, Missouri.

Paratype. Urban & Kline (1970, pl. 18, fig. 3).

Material. Eighteen specimens from samples MW 25.4 and 39.9. The specimens are broken and the ornamentation is greatly eroded.

Measurements. Taken from four specimens from samples MW 25.4 and 39.9. L 117–156.4 (Av. 131.9); Le 75–109 (Av. 88); Ln 42–48 (Av. 43.9); Dmax 67–84 (Av. 72.8); Dn 25.5–30 (Av. 27.4); Lsp 3.2–4.5 (Av. 3.9); Ln/L 0.3–0.35; L/Dmax 2.2–2.7.

Diagnosis. Shape same as *Ancyrochitina spinosa* (s.s.); neck cylindrical at base, swelling near middle and expanding slightly at aperture.

Description. A variety of *Ancyrochitina spinosa* with a conical to elongate club-shaped chamber, with a gentle but definite flexure. The chamber narrows considerably to a relatively short, cylindro-conical neck. The main feature of this new variety is the presence of a swelling near the middle of the neck; the base of the neck is a narrow cylinder but this expands slightly, giving an inflated appearance around what may be the prosome. After this 'bump' the neck continues either as a broad tube or as a cone. A fringed, slightly flared collar encircles the aperture. The chamber base varies from flat to convex, with a well rounded basal edge.

A relatively dense covering of spines is randomly distributed over the vesicle surface. These spines may be simple, bifurcate or multifurcate, some with broad bases. Smaller, finer spines may be observed on the neck.

Remarks. Due to the generally poor preservation of specimens from Martins Well, the holotype for this new variety has been chosen from the first specimens described with the unusual form of the neck (Urban & Kline 1970). This feature is quite obvious in some individuals but flattening of the neck may obscure its presence in others. Although a minor difference, the neck swelling appears to be a consistent feature within the populations where it is found. At this stage no stratigraphic significance is attributed to its distribution.

This new variety can also be distinguished by its slightly shorter neck; e.g. Ln/L = 0.3–0.35 from Martins Well, 0.35–0.38 from the Cedar City Formation (measured from Urban & Kline 1970, pl. 18, figs 1–2), 0.42–0.43 from the Baltic (measured from Eisenack 1959, pl. 2, figs 1–2), whereas Dunn (1959) reported a range of 0.4–0.47. Shorter, finer spines on the neck also differentiate this variety from typical members of the species.

Poor preservation of ornamentation on the Martins Well specimens makes it impossible to demonstrate the existence of 'antler-like' spines mentioned by Eisenack (1932) and Urban & Kline (1970). The Martins Well material has generally shorter spines than those depicted by Urban & Kline (1970) and Eisenack (1959), but Eisenack (1964) noted that specimens with reduced spines made up some of the population of *Anc. spinosa* and the same degree of intraspecific variation may apply here.

Anc. spinosa appears to have a very long stratigraphic range, from the Silurian to the Middle Devonian. This is paralleled by the occurrence of this new variety.

Fig. 8. A–E, *Gotlandochitina kutjala* n. sp., MW 18.6. A, D, holotype QMF 25492, × 300, and enlargement of chamber wall showing spine form and density × 900. B, C, paratype QMF 25493, ×300, and enlargement of chamber wall and ornamentation × 1300. E, paratype QMF 25494, × 300. F, G, *Gotlandochitina* sp. A, QMF 25495, × 400, and enlargement of broken chamber wall displaying ornamentation × 1000, MW 39.9. H, *Ancyrochitina spinosa* var. *gibba* n. var., broken specimen QMF 25496, × 350, MW 24.6. I, *Bursachitina mawsonae* Winchester-Seeto, QMF25497, × 300, MW 49.

Genus Angochitina Eisenack, 1931

Type species. Angochitina echinata Eisenack, 1931.

Angochitina cactula n. sp.

Fig. 9A–E

? *Angochitina* cf. *A. crassispina* Eisenack.—Wrona 1980: 129, pl. 27, figs 1–6.

Etymology. A diminutive of 'cactus', from the Latin for a prickly plant, referring to the form of the spines.

Holotype. QMF 25476, Fig. 9A.

Type horizon and locality. MW 49, 55m above the base of the MW section of the Martins Well Limestone, Shield Creek Formation, Broken River area of north Queensland.

Paratypes. QMF 25477, Fig. 9B–C; QMF 25478, Fig. 9D–E.

Other material. Thirteen specimens from samples MW 34.2, 39.9 and 49.

Measurements. Taken from ten specimens from samples MW 34.2, 39.9 and 49. L 141–166.5 (Av. 152); Lc 85–107 (Av. 91.6); Ln 55–74.6 (Av. 63); Dmax 44–73 (Av. 60.6); Dn 26–38 (Av. 28.8); Lsp 3–25 (Av. 12.1); Ln/L 0.4–0.46; L/Dmax 2.1–2.9.

Diagnosis. Chamber subcylindrical to elongate elliptical; neck subcylindrical to conical; strong, thorn-like spines sparsely distributed over vesicle surface.

Description. The chamber shape varies considerably; though most commonly an elongate ellipse, flattening or partial flattening may produce a conical to almost rectangular form. This distortion may also affect the base, giving a convex, chevron or even flat aspect. Flexure is very elongate, and the position of the base of the neck is often difficult to determine. The subcylindrical to conical neck occupies less than half the total vesicle length and is topped with a conspicuous, fringed collar.

Ornamentation consists of a sparse covering of strong, broad-based, thorn-like spines that are mostly simple, but rare bifurcate spines can be observed. Some spines are curved towards the aperture. The spines and broken spine bases appear to be randomly distributed over the vesicle surface, with little evidence of a linear arrangement. The spines occur predominantly on the chamber, base and lower neck; those on the upper neck are reduced in length and thickness.

Remarks. In spine form and distribution, *A. cactula* is strikingly similar to *A.* cf. *A. crassispina* depicted by Wrona (1980). The only difference lies in the larger size of the Polish species and in its slightly longer neck; as this is considered to have no taxonomic significance, Wrona's form has been tentatively placed in *A. cactula.*

A. crassispina Eisenack shows a number of similarities to *A. cactula*, especially in vesicle shape. Differences in ornamentation, including a greater number of spines, a concentration of spines on the lower part of the neck and a paucity of lambda-shaped spines, serve to differentiate *A. cactula.*

Eisenack (1964) discussed the close relationship between *A. crassispina, A. echinata* Eisenack, *A. filosa* Eisenack and other species, placing them together with intermediate forms in a 'Formengruppe'. *A. cactula* shows a number of similarities with this 'Formengruppe'. Intraspecific variation in chamber shape and spine density of all the groups makes species assignment difficult, especially when based on a small number of specimens. This is further hampered by the problem that Eisenack's photographs are only silhouettes, making comparisons of ornamentation very difficult. Despite the resemblance of the Queensland specimens to *A. filosa* as depicted by Eisenack (1968) and Wrona (1980), they are assigned to a new species because of the presence of predominantly broad-based spines, the greater number of neck spines and the comparatively short neck.

Angochitina cf. A. callawayensis Urban & Kline, 1970

Fig. 10D, E

Angochitina cf. *A. callawayensis.*—Paris 1976: 95, pl. 19, fig. 9, pl. 26, fig. 5.—Winchester-Seeto 1993: fig. 6.8–6.9.

Material. Twenty-three specimens from samples MW 24.6 and 39.9.

Measurements. Taken from five specimens from samples MW 24.6 and 39.9. L 119–150 (Av. 133.5); Lc

Fig. 9. A–E, *Angochitina cactula* n. sp., MW 49. A, holotype QMF 25476, × 350. B, C, paratype QMF 25477, × 300, and enlargement of neck × 600. D, E, paratype QMF 25478, × 300, and enlargement of neck × 900. F, *Angochitina* sp. A, QMF 25479, × 350, MW 18.6. G, H, *Angochitina* aff. *A. crassispina* Eisenack, QMF 25480, × 350, and enlargement of vesicle wall × 1500, MW 24.6. I, *Angochitina* sp. E, QMF 25481, × 300, MW 39.9.
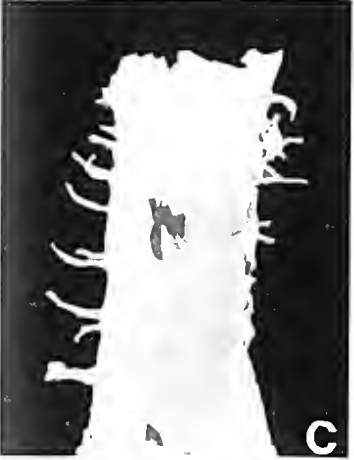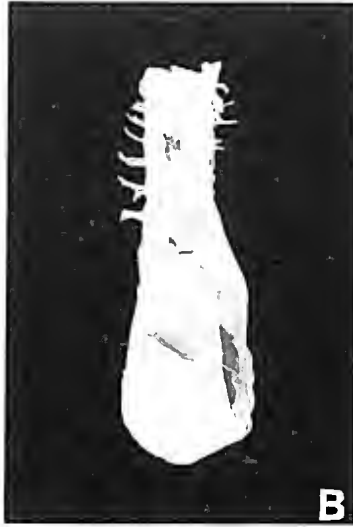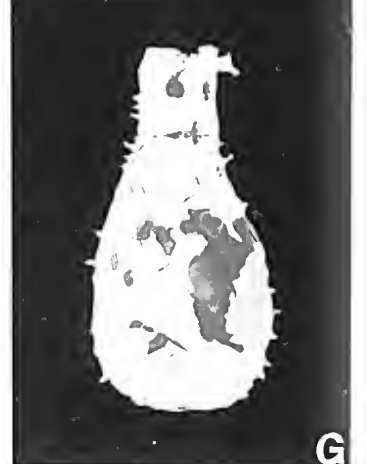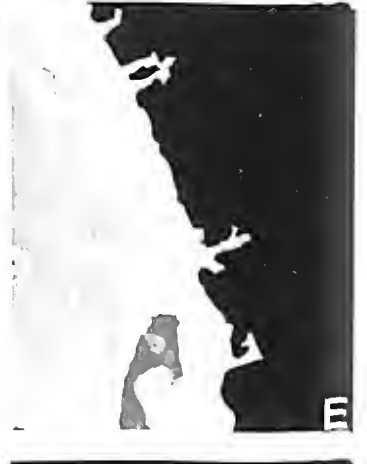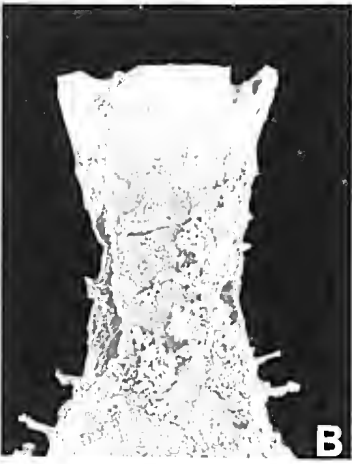
84–93 (Av. 87.6); Ln 38–57 (Av. 46.2); Dmax 52–60 (Av. 55.6); Dn 24–32 (Av. 27.8); Lsp 5–7.5 (Av. 6.6); Ln/L 0.24–0.38; L/Dmax 2.3–2.6.

Remarks. The silhouette and the presence of fine, wispy, bizarre-shaped spines is strongly reminiscent of *A.* cf. *A. callawayensis* from the Garra Limestone (Winchester-Seeto 1993). Specimens from Martins Well have shorter spines but this may reflect the poor preservation. Both the Garra specimens and those from Martins Well have more slender, ovoid vesicles than those figured by Paris (1976).

No alignment of spines is observed on individuals from Martins Well. Many spines display very fine distal terminations; several on each specimen are bent, forked or T-shaped close to the tip of the spine, a characteristic feature of this species in both the Garra Limestone and Martins Well sections.

Angochitina comosa Taugourdeau & Jekhowsky, 1960

Fig. 10A, B

Angochitina comosa Taugourdeau & Jekhowsky 1960: 1221, pl. 3, figs 33–35.—Grignani 1967: pl. 1, fig. 18.—Magloire 1967: pl. 3, fig. 18.—Diez & Cramer 1978: 207, pl. 1, fig. 16.—Rahmani 1978: 278, pl. 2, figs 7, 8.—Paris in Chlupáč et al. 1985: pl. 3, fig. 13.—Winchester-Seeto 1993: fig. 6.13–6.15.
Angochitina cf. *A. comosa.*—Paris 1976: 95, pl. 19, figs 1, 2.
? *Angochitina echinata.*—Eisenack 1972a: 71, pl. 17, figs 1–14.

Material. Seventy-five specimens from samples MW 18.6, 20.9, 25.4, 39.9 and 95.6.

Measurements. Taken from fifteen specimens from samples MW 18.6, 20.9, 25.4, 39.9 and 95.6. L 114.7–159.1 (Av. 140.4); Le 75–100.8 (Av. 87); Ln 29.6–78.2 (53.5); Dmax 47.6–69.6 (Av. 60.9); Dn 21–37.4 (Av. 32.6); Lsp 3.4–7.2 (Av. 5.3); L/Dmax 1.9–2.7; L/Ln 2.5–2.9.

Remarks. The specimens from Martins Well resemble those from the Garra Limestone in New South Wales (Winchester-Seeto 1993) and fall readily into the range of dimensions determined for the Garra specimens. Small differences in ornamentation on the Martins Well specimens include a slightly lower spine density (4–6 per 100 μm²) and rare bifurcate spines scattered

amongst the simple ones, thus contrasting with the New South Wales material in which bifurcate spines are more common. The individual spines also appear to be thicker than those from the Garra Limestone but this may reflect preservation and the organic 'glue' that covers many specimens.

Angochitina aff. A. crassispina Eisenack, 1964

Fig. 9G, H

Angochitina aff. *crassispina* Eisenack.—Winchester-Seeto 1993: fig. 7.8.

Material. Fifteen specimens from samples MW 22.6, 24.6, 25.4, 30.0, 49 and 95.6.

Measurements. Taken from four specimens from samples MW 24.6, 49 and 95.6. L 138–163 (Av. 147.3); Le 88.5–96 (Av. 92.4); Ln 45–68 (Av. 53.6); Dmax 63–68 (Av. 65.5); Dn 26–30 (Av. 27.6); Lsp 9–12 (Av. 10.4); Ln/L 0.3–0.42; L/Dmax 2.2–3.0.

Remarks. The vesicle surface has a small number of irregularly scattered, robust spines. These are predominantly simple but are interspersed with rare bifurcate, multifurcate and lambda-shaped spines. This ornamentation is close to that described by Eisenack (1964) and Laufeld (1974) for *A. crassispina.*

The main difference between *A.* aff. *A. crassispina* and *A. crassispina* lies in the much smaller size of the former and its proportionally shorter neck (i.e. less than half the total length of the vesicle). This comparison is true also for the specimens of *A.* cf. *A. crassispina* described from Poland by Wrona (1980).

Specimens of *A.* aff. *A. crassispina* from Martins Well are larger than those from the Garra Limestone and the ornamentation is denser.

Angochitina dimorpha Taugourdeau & Jekhowsky, 1960

Fig. 10F, G

Angochitina dimorpha Taugourdeau & Jekhowsky 1960: 1221, pl. 3, figs 38–40.

Material. Eighty-seven specimens from samples MW 15.0, 18.6, 24.6, 25.4, 34.0, 39.9, 49 and 95.6.

Measurements. Taken from nine specimens from samples MW 18.6, 24.6, 25.4, 39.9, 49 and 95.6. L 117–144 (Av. 128); Le 70–105 (Av. 88.6); Ln 28–52

Fig. 10. A–C, *Angochitina comosa* Taugourdeau & Jekhowsky. A, B, QMF 25470, × 350, and enlargement of neck and collarette × 900, MW 25.4. C, QMF 25471, × 300, MW 18.6. D, E, *Angochitina* cf. *A. callawayensis* Urban & Kline, QMF 25472, × 350, and enlargement of vesicle wall showing spine form × 1500, MW 24.6. F, G, *Angochitina dimorpha* Taugourdeau & Jekhowsky, a form with no collar QMF 25473, enlargement of neck × 1100, and × 350, MW 24.6. H, *Angochitina* sp. C, QMF 25474, × 350, MW 34.2. I, *Angochitina hypenetes* Winchester-Seeto, QMF 25475, × 350, MW 39.9.

(Av. 39.3); Dmax 57–65 (Av. 60.6); Dn 23–32 (Av. 28.1); Lsp 3–7 (Av. 4.8); Ln/L 0.2–0.42; L/Dmax 1.9–2.4; Dn/Dmax 0.38–0.5.

Description. *A. dimorpha* is a relatively small species of *Angochitina* with an oval, club-shaped to subcylindrical chamber. The maximum diameter is in the lower third of the vesicle but rarely at the basal edge. Flexure is gentle and generally indistinct, leading to a short, cylindrical neck; some individuals have a short, slightly flared collar. The base is strongly convex and the aboral margin is broadly rounded.

Short, robust thorn-like spines cover the entire vesicle surface; many spines are curved. The ornamentation is relatively sparse (3–4 spines per 100 μm^2).

Remarks. Taugourdeau & Jekhowsky (1960) stressed an apparent difference between forms with a collar (e.g. their fig. 38) and those without (their figs 39, 40), hence the name *dimorpha*. This distinction is observed in specimens from Martins Well, but a number of intermediate forms suggest that the disparity is not as marked as that suggested by Taugourdeau & Jekhowsky.

In other respects, such as spine form and distribution, the two populations from the Sahara and Australia are very similar.

Angochitina hypenetes Winchester-Seeto, 1993

Fig. 10I

Angochitina hypenetes Winchester-Seeto 1993: fig. 7.1–7.5.

Material. A single specimen from sample MW 39.9.

Measurements. L 147; Lc 96; Ln 51; Dmax 58.5; Dn 25; Lsp 5.6; Ln/L 0.35.

Remarks. Surface ornamentation is largely obscured by an organic coating, so spine density is difficult to establish; all other features, however, are consistent with *A. hypenetes* from the Garra Limestone (Winchester-Seeto 1993).

Angochitina sp. A

Fig. 9F

Angochitina sp. B.—Winchester-Seeto 1993: fig. 7.10–7.15.

Material. Seven specimens from samples MW 18.6, 24.6, 25.4 and 49.

Measurements. Taken from all seven specimens. L 125–147 (Av. 139.7); Lc 78–99 (Av. 91); Ln 43–54.4 (Av. 48.6); Dmax 46–68 (Av. 53.3); Dn 24–34.4 (Av. 28.6); Lsp 4–8 (Av. 5.9); Ln/L 0.31–0.41; L/Dmax 2.1–3.1.

Remarks. The present occurrence extends the range of the species into Assemblage 2 from the Garra Limestone (Winchester-Seeto 1993).

Angochitina sp. B

Fig. 7A–E

Material. One hundred and one specimens from samples MW 13.7, 18.6?, 20.9, 24.6, 25.4, 30.0, 39.9, 49 and 51.

Measurements. Taken from 15 specimens from samples MW 18.6, 24.6, 25.4, 39.9 and 49. L 114–163 (Av. 126.8); Lc 66–96.2 (Av. 80.3); Ln 30–72 (Av. 55); Dmax 43–71.4 (Av. 58.2); Dn 18–30 (Av. 23.7); Dcoll 24–42 (Av. 33); Lsp 2.5–11.0 (Av. 7.2); Ln/L 0.26–0.52; L/Dmax 1.9–3.2; Dmax/Dn 2.1–3.0. Note that Ln/L varies considerably because of difficulties in determining the boundary of the neck and the chamber due to the very elongate flexure.

Description. A species of *Angochitina* with an ovoid to pyriform chamber and an elongate flexure leading to a relatively short neck. The neck is surmounted by a wide collar that is greatly expanded at the aperture (Dn/Dcoll = 0.5–0.88).

The vesicle has a sparse scattering of spines, generally very fine on the collar and neck, becoming more robust on the chamber. Rare bifurcate spines may be present on the neck, but those on the chamber consist predominantly of simple, broad-based spines with an almost triangular shape, giving a thorn-like aspect. Near the basal edge many of the spines take on a node-like appearance.

Remarks. The characteristic node-like appearance of the spines near the basal edge may be partly due to spine breakage and secondary infilling. Better preserved specimens are required for confirmation, so this species has been kept in open nomenclature.

A. comosa has a similar guise but differs in having a more spheroid chamber, a highly convex base, a rounded basal edge and a slightly narrower aperture (see Fig. 11 relating total length to the ratio Dmax/Dn.) The ornamentation of *A. comosa* is much denser and consists of many bifurcate spines on the chamber, with no evidence of 'nodes' or triangular spines near the basal edge.

Many individuals of *Sphaerochitina sphaerocephala* (Eisenack) resemble *Angochitina* sp. B in shape (e.g. Eisenack 1955, pl. 1, figs 5, 6), but no spinose ornamentation has been reported in the former species.
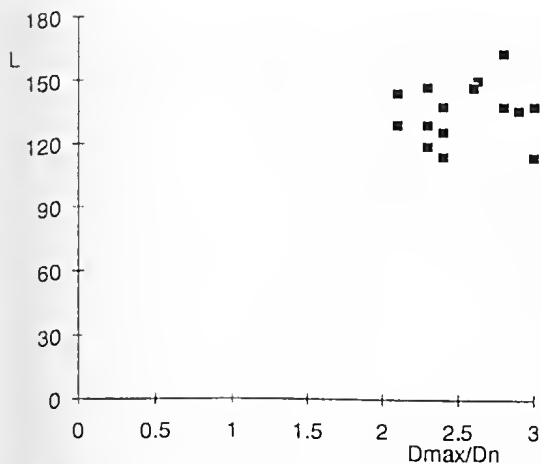
Fig. 11. Intraspecific variation in *Angochitina* sp. B; L = length of vesicle, Dmax/Dn = maximum diameter of vesicle/diameter of neck.

Angochitina sp. C

Fig. 10H

Material. Thirty-five specimens from samples MW 25.4, 34 and 34.2.

Measurements. Taken from five specimens from samples MW 25.4 and 34.2. L 129–146 (Av. 138.8); Le 69–84 (Av. 80.7); Ln 45–75 (Av. 58.1); Dmax 48–60 (Av. 52.8); Dn 22.5–30 (Av. 26.1); Lsp 2.5–5 (Av. 3.3); Ln/L 0.35–0.52; L/Dmax 2.1–3.0; Dn/Dmax 0.37–0.59.

Description. A species of *Angochitina* with a chamber that varies from spheroidal to a slender oval shape. The basal edge is broadly rounded and the base is convex. Flexure is indistinct; the chamber tapers gently to a quite narrow, nearly cylindrical neck with a very slight flare at the aperture. The neck occupies one-third to one-half the total length. Short, fine spines, ranging from simple to bifurcate in form, cover all of the vesicle, except the edge of the collar.

Remarks. The highly variable vesicle shape matches the range depicted by Eisenack for *Sphaerochitina sphaerocephala,* especially those specimens designated as intermediate between *S. sphaerocephala* and *S. acanthifera* (Eisenack 1972b, pl. 28, figs 21, 22). Eisenack (1964) referred without accompanying illustrations to a similar complex from Gotland.

The existence of very fine spines on *Angochitina* sp. C rules out assignment to *S. sphaerocephala* which is generally smooth or possesses only tubercles (Eisenack 1932). *S. acanthifera*

has short spines, but its characteristic 'bend' at the maximum diameter of the chamber is found in only a few specimens of *Angochitina* sp. C. The Queensland material has been placed in *Angochitina* because of the presence of sparsely distributed spines as opposed to tubercles or dense erect spines as found on *Sphaerochitina* (Eisenack 1955).

Angochitina hypenetes also resembles this species but has shorter, finer spines more sparsely distributed on the vesicle, and lacks evidence of a distinct collar.

Angochitina sp. D

Fig. 12F, G

Material. One partially flattened specimen from sample BOO 28.

Measurements. L 107; Le 39; Ln 68; Dmax 65; Dn 20; Lsp 12; Ln/L 0.36; L/Dmax 2.35.

Description. This small specimen has been badly distorted by flattening. The chamber has an almost square aspect, with a flat base but a rounded basal edge. Flexure is ill-defined, leading to a short neck that narrows slightly towards the aperture. There is a small collar with a crenulate edge.

The spinose ornamentation is distinctive but its distribution is difficult to determine due to poor preservation leaving few spines on the chamber. The neck spines are substantial and relatively thick, ranging in form from simple to bifurcate. The bifurcate spines may be broad-based as a result of the coalescence of two spines or may be raised slightly from the vesicle surface by a short stalk.

Remarks. It is possible that this species belongs to *Gotlandochitina* but the presence of a linear arrangement of spines on the chamber cannot be confirmed in this single specimen. The peculiar ornamentation distinguishes the species from any other of similar size or shape.
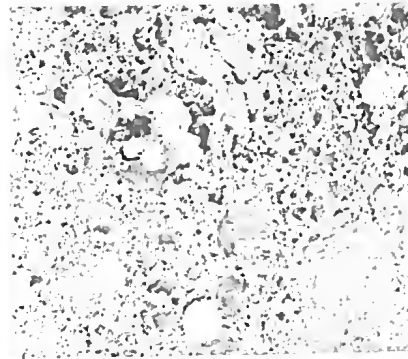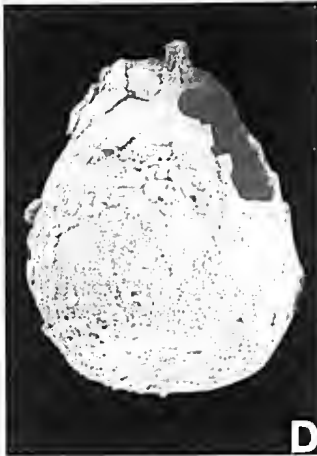
Angochitina sp. E

Fig. 9I

Material. One specimen from sample MW 39.9.

Measurements. L 219; Le 86; Ln 133.3; Dmax 64.5; Dn 30; Ln/L 0.6.

Description. This species has a narrow, chevron-shaped chamber with a convex base and no apparent basal edge. An indistinct flexure leads to a relatively long neck occupying more than half of the total vesicle length. The neck is subcylindri-

cal in form but exhibits variable width along its length due to flattening and twisting; this feature may be teratological in nature. A small collar may be present, flaring slightly towards the aperture.

Spinose ornamentation on the vesicle consists of relatively short spines that may be simple or lambda-shaped. Spines are reduced in length and number on the neck, with very few appearing on the upper part of the neck.

Remarks. This single individual may be merely an aberrant form of *A.* aff. *A. crassispina*, as suggested by the presence of a number of lambda-shaped spines.

Angochitina sp. E also exhibits many similarities to *A. longicolla*, described from the Baltic Silurian by Eisenack (1959). The general shape, size and proportions of *A. longicolla* match those of the Australian specimen (e.g. the proportion L/Dmax is 3.2–3.5 in the specimens figured by Eisenack and is 3.4 in the Australian specimen). This similarity is reinforced by the presence of lambda-shaped spines on both groups. The only differences are the reduced number of spines and the slightly longer neck of the Australian specimen; Ln/L is 0.6 in the Martins Well specimen, whereas in the specimens figured by Eisenack (1959, pl. 2, figs 8, 9) Ln/L ranges from 0.47 to 0.5.

This species is also similar in shape to *Angochitina* sp. 2 of Paris (1976) and to *A.* cf. *A. longicollis* described by Wrona (1980), but, as neither Paris nor Wrona figured specimens with well-preserved ornamentation, the similarities are difficult to substantiate.

Genus **Bulbochitina** Paris, 1981a

Type species. Bulbochitina bulbosa Paris, 1981a.

Bulbochitina bulbosa Paris, 1981a

Fig. 12A–E

Bulbochitina bulbosa Paris 1981a: 134–135, pl. 35, figs 1–8, 10–19, pl. 37, fig. 1.

Material. Twenty-five specimens from samples BOO 13.1 and BOO 17.8.

Measurements. Taken from eleven specimens from sample BOO 13.1. L 111–158 (Av. 128.8); Dmax 107–165 (Av. 128.5); Da 41–80 (Av. 57.5); L/Dmax 0.79–

1.4; Da/Dmax 33–50%. See Fig. 13 for a graph relating total length of the vesicle (L) to maximum diameter of the vesicle (Dmax).

Remarks. One specimen (Fig. 12B) has what appears to be the remnant of a basal carina, but no other individual of this population displays this character. In general the basal margin of most specimens of *Bu. bulbosa* from Boola Quarry is well rounded. The presence of a carina, which distinguishes the genus *Armoricochitina*, is very difficult to observe if the feature has been eroded, but generally the aboral margin of *Armoricochitina* is relatively sharp and more abrupt than is observed on the specimens from Boola Quarry.
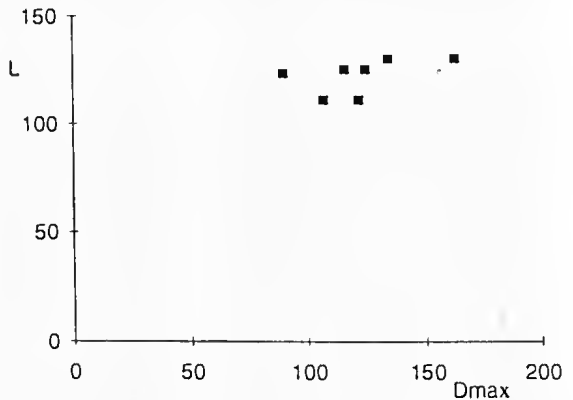
Fig. 13. Intraspecific variation in *Bulbochitina bulbosa* Paris, 1981a; L = length of vesicle, Dmax = maximum diameter of vesicle.

Genus **Bursachitina** Taugourdeau, 1966

Type species. Desmochitina bursa Taugourdeau & Jekhowsky, 1960.

Bursachitina mawsonae Winchester-Seeto, 1993

Fig. 8I

Bursachitina mawsonae Winchester-Seeto 1993: 748, fig. 9.1–9.8.

Material. Twelve specimens from samples MW 20.9, 49, 69, 74, 78.6 and 95.6.

Measurements. Taken from two specimens from samples MW 49 and MW 95.6. L 142.8–155; Dmax 85–92; Da 63–71.5; Da/Dmax 74–77%.

Fig. 12. A–E, *Bulbochitina bulbosa* Paris, BOO 13.1. A, NMV P137603, × 300. B, NMV P137604, × 300. C, NMV P137605, × 300. D, E, NMV P137606, × 300, and enlargement of chamber wall showing ornamentation, × 1000. F, G, *Angochitina* sp. D, small, partially flattened specimen NMV P137607, × 400, and enlargement of neck showing detail of neck spines, × 1400, BOO 28. H, *Gotlandochitina* sp. B, NMV P137608, × 350, BOO 17.8. I, *Bursachitina* sp., NMV P137609, × 300, BOO 13.1.

Remarks. The vesicle shapes of *Desmochitina parkerae* Urban and *B. mawsonae* are superficially quite similar. The material from Martins Well contains slightly larger specimens of *B. mawsonae* than those from the Garra Limestone, placing them in the size range of *D. parkerae*. The diameter of the oral opening, however, serves to differentiate the two taxa; the aperture of the Martins Well specimens is approximately 75% of the maximum diameter of the vesicle, much less than 80–90% found in *D. parkerae*.

The specimen in Fig. 8I represents one extreme of intraspecific variation, where the maximum diameter is only 55% of the total length of the vesicle. This feature is common to individuals of this species from Martins Well and fits within the range of shapes from the type locality in the Garra Limestone. More typical members of *Bursachitina* have a maximum diameter closer to that of the length of the vesicle, but the amended diagnosis given by Paris (1981a: 137) does not exclude the forms observed from Martins Well.

Bursachitina sp.

Fig. 12I

Material. Five specimens from sample BOO 13.1.

Measurements. Taken from two specimens. L 140.5–153.5; Dmax 115–118; Da 53–55.5; L/Dmax 1.2–1.4; Da/Dmax 0.46–0.47.

Description. This species has a conical to ovoid vesicle, with weak to moderately convex flanks. Maximum diameter occurs in the lower half to lower third of the length of the vesicle, but not at the aboral margin. The aperture is quite narrow, less than 50% of the maximum diameter, and is surrounded by a short collar with a crenulate edge. The broadly rounded basal edge leads to a flat or concave base, displaying a large basal callus. Ornamentation is poorly preserved but appears to be felt-like, with no evidence of spines.

Remarks. The general appearance of this species is reminiscent of *Bursachitina maritima* (Paris), especially the broadly rounded aboral margin

and the basal scar. Ornamentation also appears to be similar, despite the poor preservation of the specimens from Boola Quarry. The vesicle shape differs in being somewhat narrower than that of *B. maritima*, thus giving a much larger apical angle (i.e. approximately 45°). The aperture is also smaller, being only 46–47% of the maximum diameter, whereas *B. maritima* has an aperture up to 54–57% of the maximum diameter. The paucity of specimens makes a conclusive identification difficult, as these may merely represent extremes of intraspecific variation.

Grignani (1967, pl. 1, fig. 27) figured a specimen, assigned to *Desmochitina urna* Eisenack, with a similar shape to the individuals from Boola. This specimen, from the Siegenian of Tunisia, may be related to the Boola group.

Despite the similarity of the outline of this species to *Armoricochitina ceneratiensis* (Paris), there is no evidence of a carina at the basal margin, thus excluding the species from *Armoricochitina*.

Genus Gotlandochitina Laufeld, 1974

Type species. Gotlandochitina martinssoni Laufeld, 1974.

Gotlandochitina implicationis (Urban, 1972)

Fig. 14A, B

Angochitina implicationis Urban 1972: 15, pl. 3, figs 1–7.—Urban & Newport 1973: pl. 1, figs 7, 8.—Winchester-Seeto 1993: 746, figs 7.6, 7.7.

Material. One specimen from sample MW 34.2

Measurements. L 114; Le 69; Ln 45; Dmax 60; Dn 24; Lsp 3.5.

Remarks. The specimen from Martins Well is smaller than those from the United States or New South Wales and has a longer, better defined neck, but clearly displays the linear arrangement of spines described by Urban (1972).

Gotlandochitina kutjala n. sp.

Fig. 8A–D

Fig. 14. A, B, *Gotlandochitina implicationis* (Urban), QMF 25487, × 350, and enlargement of lower part of chamber showing linear arrangement of ornamentation × 1200, MW 34.2. C, D, *Gotlandochitina* cf. *G. marettensis* Paris, QMF 25488, × 350, and enlargement of lower part of chamber showing details of ornamentation × 600, MW 49. E–G, *Gotlandochitina marettensis* Paris. E, F, QMF 25489, × 350, and enlargement of chamber wall showing ornamentation and 'holes' that may indicate the presence of parasites × 900, MW 25.4. G, QMF 25490, × 350, MW 24.6. H, I, *Gotlandochitina* aff. *G. philipotti* (Paris); QMF 25491, enlargement of chamber wall × 650, and × 350, MW 39.9.

Etymology. Named for the Kutjala, one of the Aboriginal tribes of the Broken River area.

Holotype. QMF 25492, Fig. 8A, D.

Type horizon and locality. MW 18.6, MW section of the Shield Creek Formation, Broken River area of Queensland.

Paratypes. QMF 25493, Fig. 8B, C; QMF 25494, Fig. 8E.

Other material. One hundred and eighteen specimens from samples MW 18.6, 22.6, 24.6, 25.4, 39.9, 49 and 78.6. The specimens are poorly preserved, none having the ornamentation intact.

Measurements. Taken from twenty-one specimens from samples MW 18.6, 24.6, 25.4, 39.9 and 49. L 88–177 (Av. 147.8, holotype 163); Lc 62–119 (Av. 94, holotype 102); Ln 25–69 (Av. 53.3, holotype 61); Dmax 44–68 (Av. 59.6, holotype 65); Dn 15.5–44 (Av. 27.5, holotype 34); Lsp 2–9.3 (Av. 5.4, holotype 7); Ln/L 0.3–0.45 (holotype 0.37); L/Dmax 2.0–3.1 (holotype 2.5).

Diagnosis. Chamber slender, elongate and club-shaped; flexure conspicuous; neck short with collar expanded at aperture. Spines short, distinct, in subparallel vertical rows.

Description. The slender, elongate, claviform vesicle has a conspicuous flexure without shoulders. The neck comprises less than half the length of the vesicle and has a clearly defined, slightly flared collar with a crenulate edge. The base is strongly convex. The shape of the chamber varies considerably, and this is further complicated by the distortional effects of compression on different parts of the chamber. The maximum diameter of the vesicle appears between the lower half to the lower third of the chamber length, so that the form of the chamber ranges from a tear-drop to a club-shape.

Ornamentation consists of short spines distributed relatively sparsely (3–5 per 100μm^2) in sub-parallel, vertical rows covering the collar, neck, chamber and base. The length of the spines is reduced on the collar. Though predominately simple in form, the spines may also be bifurcate or multifurcate. Curvature is common among the simple spines.

Remarks. In shape and dimensions, *G. kutjala* closely matches the specimens depicted by Urban (1972) as *Angochitina capillata* Eisenack, and by Lange (1967) and Winchester-Seeto (1993) as *A.* cf. *A. capillata* Eisenack. The differences lie in the sparser ornamentation of *G. kutjala* and in the relatively finer spines.

The ornamentation of *G. kutjala* resembles
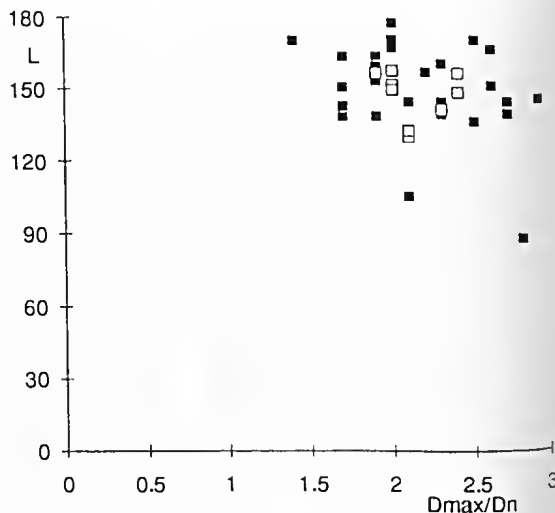
Fig. 15. Intraspecific variation in *Gotlandochitina kutjala* n. sp. (black squares) and *G. marettensis* Paris. 1981b (white squares); L = length of vesicle, Dmax/Dn = maximum diameter of vesicle/diameter of neck.

that of *Angochitina filosa* Eisenack as illustrated by Wrona (1980), but the former may be distinguished by its shorter neck. *Angochitina echinata* Eisenack (see Eisenack 1931, 1972a; Laufeld 1974; Wrona 1980) may also be confused with *G. kutjala*, but *A. echinata* has a more spherical chamber quite unlike that of *G. kutjala*.

In each of the above examples of similar species, the illustrations and descriptions give no indication of a linear arrangement of the spines. *Gotlandochitina marettensis* Paris is probably the closest species in this regard, but it differs from *G. kutjala* in having longer, more complex spines and a more spherical chamber with the maximum diameter approximately halfway down the length of the chamber. Fig. 15 illustrates the close similarity between *G. kutjala* and *G. marettensis* in a graph of the total length (L) versus maximum diameter of chamber/diameter of neck (Dmax/Dn).

Gotlandochitina marettensis Paris, 1981b

Fig. 14E–G

? *Angochitina bifurcata* Collinson & Schwalb 1955: 21–22, pl. 2, figs 1–3.—Costa 1967: 97, pl. 1, fig. 9.—Costa 1971: 224, fig. 14.

? *Angochitina* sp.—Paris 1977: 122, pl. 6–16, fig. 14.

Gotlandochitina cf. *G. bifurcata.*—Paris 1978: pl. 1, fig. 7.

Gotlandochitina marettensis Paris 1981b: 63–65, pl. 5, figs 1, 2, 5, 9, 10.—Paris 1981a: 265, pl. 36, figs 3, 4, 16.

Material. Fifty-four specimens from samples MW 20.9, 22.6, 24.6, 25.4, 30, 39.9 and 49.

Measurements. Taken from nine specimens from samples MW 24.6, 25.4, 39.9 and 49. L 129.5–157 (Av. 146.6); Lc 78–108 (Av. 94.3); Ln 45–64 (Av. 52.0); Dmax 48–70 (Av. 62.6); Dn 18–34 (Av 28.1); Lsp 2–10.2 (Av. 7.2); Ln/L 0.3–0.41; L/Dmax 2.2–3.1.

Remarks. The shape and dimensions of the specimens from Martins Well closely match those from France (Paris 1981b). Poor preservation of ornamentation makes determination of maximum spine length difficult and assessment of the presence of rows of spines (as opposed to irregularly scattered spines) impossible. Spinose ornamentation consists predominantly of simple and bifurcate spines, but the apparent lack of multifurcate spines may also be related to preservation. Poor preservation may also explain the much shorter spines found on the Australian specimens (i.e. less than half the average length of the spines in the French specimens). It is also possible that the shorter spines represent a regional variation of the species.

Paris (1981b) noted the similarities between *G. marettensis* and *Angochitina bifurcata* Collinson & Schwalb from North and South America. Minor differences in *G. marettensis* include the presence of simple spines amongst the bifurcate ones and a slightly larger vesicle. It is not possible to judge from the illustrations provided by Collinson & Schwalb (1955) or Costa (1971) whether the spines on *A. bifurcata* are arranged in rows. Thus, the relationship between *A. bifurcata* and *G. marettensis* cannot yet be resolved. However, the similarities are so striking that if the two species are not conspecific, then there must be some evolutionary connection.

This is the first report of *G. marettensis* from the Pragian; however, *A. bifurcata* is known from the Lochkovian.

Gotlandochitina cf. G. marettensis? Paris, 1981b

Fig. 14C, D

? *G.* cf. *G. marettensis.*—Paris 1979: 353, fig. 1 (*nomen nudum*).—Paris 1981b: 65, pl. 5, figs 12, 15.

Material. Three specimens from sample MW 49.

Measurements. Taken from two of the specimens. L 141; Lc 84–90; Ln 51–57; Dmax 48–57; Dn 19–27; Lsp 15–24; Ln/L 0.36–0.4; L/Dmax 2.5–2.9.

Remarks. The shape, dimensions and ornamentation of these specimens are almost identical with *G.* cf. *G. marettensis* of Paris, except for a coronet of spines at the aperture on specimens from Martins Well. *G.* cf. *G. marettensis* may be merely an extreme variant of *G. marettensis*, a suggestion supported by the fact that the two forms are present at both Martins Well and Le Lezais, Gahard. This is the first report of this species from the Pragian.

Gotlandochitina aff. G. philipotti (Paris, 1976)

Fig. 14H, I

Material. Twenty-two specimens from samples MW 18.6, 30, and 39.9.

Measurements. Taken from four specimens from MW 18.6 and 39.9. L 129–139 (Av. 135); Lc 81–90 (Av. 87); Ln 48–69 (Av. 53.5); Dmax 60–63.8 (Av. 61.2); Dn 24–33 (Av. 29); Lsp 3.2–9 (Av. 6.9); Ln/L 0.35–0.37; L/Dmax 2.2–2.3; apical angle 47°–57°.

Description. Chamber shape varies from spheroid to ovoid, with a well rounded basal edge and a weak to strongly convex base. This is topped with a relatively short, cylindrical neck and may have a collar expanded at the aperture. The flexure is elongate, and shoulders are present but weak.

Fine, short spines cover the neck and collar. The ornamentation on the chamber consists of strong spines, ordered in rows, stretching from the basal edge to the base of the neck. The spines are most obvious at the middle of the chamber and tend to be shorter and less dense near the basal edge. Spines may be simple but are more commonly bifurcate or multifurcate with wide or coalesced bases; they are frequently tangled at the distal end.

Remarks. The specimens from Martins Well have a very similar spine form to that illustrated for *G. philipotti* by Chlupáč et al. (1985, pl. 3, figs 11, 12), and also conform very closely to the description and dimensions given by Paris (1976). Differences lie in the distribution and size of the ornamentation. Fine, short spines are found on the neck of specimens from Martins Well, contrasting with the fairly robust spines of European specimens, and there is no evidence of a gap in ornamentation between the spines on the neck and those on the chamber, a distinctive feature of *G. philipotti*.

Gotlandochitina sp. A

Fig. 8F, G

Material. Nine specimens from samples MW 24.6, 25.4? and 39.9.

Measurements. Taken from three specimens from samples MW 24.6, 25.4? and 39.9. L 120–167 (Av. 141.6); Lc 75–92 (Av. 84.6); Ln 44–75 (Av. 56.7); Dmax 52–65 (Av. 58); Dn 23–34 (Av. 29); Ln/L 0.37–0.45; L/Dmax 2.3–2.6.

Description. This species has an ovoid–cylindrical vesicle with a long, slender chamber, a convex base and no obvious basal edge. The neck is cylindrical to subcylindrical and occupies one-third to one-half of the total length of the vesicle.

Spines occur in a number of rows on the chamber, possibly extending onto the base (poor preservation makes this observation equivocal). The few spines left intact range from rare, simple spines, to more common bifurcate spines in antler shapes, to bifurcate spines with broad bases. Ornamentation occurs on all parts of the neck including the collar, and is generally smaller and sparser than that on the chamber.

Remarks. The shape of *Gotlandochitina* sp. A is difficult to determine as all of the specimens show some degree of distortion and breakage. There are a number of similarities in ornamentation with *Gotlandochitina villosa* Laufeld. Both the long branched spines near the aboral part of the chamber and the broad-based bifurcate spines figured by Laufeld (1974, fig. 56C, D) are also present in some individuals from Queensland. In addition, Laufeld's observation that the spines on the aboral part of the chamber tend to curve towards the oral part of the vesicle also applies to *Gotlandochitina* sp. A. The species from Queensland, however, has a denser ornamentation covering all of the neck including the collar.

Gotlandochitina sp. B

Fig. 12H

Gotlandochitina sp. C.—Winchester-Seeto 1993: 754, fig. 10.3.

Material. Three specimens from samples BOO 17.8 and 28.

Measurements. Taken from two specimens from BOO 17.8 and 28. L 123–160; Lc 66–95; Ln 57–65; Dmax 57–82; Dn 27–37; Lsp 9–17; L/Ln 2.2–2.5; Dmax/Dn 2.1–2.2.

Remarks. The three individuals from Boola Quarry differ only slightly from those found in the Garra Limestone (Winchester-Seeto 1993). A small number of thick, simple and bifurcate spines dominate the vesicle. The ornamentation is slightly longer on specimens from Boola Quarry, and between the large spines a number of small, very fine spines occur. One individual shows evidence of a row of thick spines encircling the neck.

Gotlandochitina sp. B can be differentiated from *Angochitina caeciliae* Paris by its generally longer vesicle and by the predominantly straight, simple spines, as opposed to the curved spines in *A. caeciliae.*

ACKNOWLEDGEMENTS

REFERENCES

BAYER, U. & McGHEE, G. R., 1989. Periodicity of Devonian sedimentary and biological pertubations: implications for the Devonian timescale. *Neues Jahrbuch für Geologie und Paläontologie. Monatshefte* 1989: 1–16.

CHLUPÁČ, I., LUKES, P., PARIS, F. & SCHÖNLAUB, H. P., 1985. The Lochkovian–Pragian boundary in the Lower Devonian of the Barrandian area (Czechoslovakia). *Jahrbuch der Geologischen Bundesanstalt* 128: 9–41.

COLLINSON, C., & SCHWALB, H., 1955. North American Paleozoic Chitinozoa. *State Geological Survey, Urbana, Report of Investigations* 186: 1–33.

COSTA, N. M., 1967. Quitinozoários Silurianos e Devonianos da Bacia Amazônica e sua correlaçao estratigráifca. *Atas do Simpósio sobre a Biota Amazônica* 1: 87–119.

COSTA, N. M., 1971. Quitinozoários Brasileiros e sua importancia estratigráfica. *Anais Acadamia Brasil Ciencias* 43: 209–272.

DIEZ, M. D. C. R. & CRAMER, F. H., 1978. Iberian chitinozoans. 2. Lower Devonian forms (La Vid Shales and equivalents). *Palinologia extraordinario* 1: 203–217.

DUNN, D. L., 1959. Devonian chitinozoans from the Cedar Valley Formation in Iowa. *Journal of Paleontology* 33: 1001–1017.

EISENACK, A., 1931. Neue Mikrofossilien des baltischen Silurs 1. *Paläontologische Zeitschrift* 13: 74–118.

EISENACK, A., 1932. Neue Mikrofossilien des baltischen Silurs 2. (Foraminiferen, Hydrozoen, Chitinozoen u.a.). *Paläontologische Zeitschrift* 14: 257–277.

EISENACK, A., 1955. Neue Chitinozoen aus dem Silur des Baltikums und dem Devon der Eifel. *Senckenbergiana lethaea* 36: 157–188.

EISENACK, A., 1959. Neotypen baltischer Silur-Chitinozoen und neue Arten. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 108: 1–20.

EISENACK, A., 1964. Mikrofossilien aus dem Silur Gotlands. Chitinozoen. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 120: 308–342.

EISENACK A., 1968. Über Chitinozoen des Baltischen Gebietes. *Palaeontographica, Abteilung A* 131: 137–198.

EISENACK, A., 1972a. Chitinozoen und anderen Mikrofossilien aus der Bohrung Leba, Pommern. *Palaeontographica, Abteilung A* 139: 64–87.

EISENACK, A., 1972b. Beiträge zur Chitinozoen-Forschung. *Palaeontographica, Abteilung A* 140: 117–130.

GAO LIAN-DA, 1986. Chitinozoans. In *Devonian Stratigraphy, Palaeontology and Sedimentary Facies of Longmenshan, Sichau*, Hou Hong-fei, ed., Chengdu Institute of Geology and Mineral Resources and Institute of Geology, Chinese Academy of Geological Sciences, Chengdu, 356–357.

GRIGNANI, D., 1967. Correlation with Chitinozoa in the Devonian and Silurian in some Tunisian well samples. *Review of Palaeobotany and Palynology* 5: 315–325.

JAGLIN, J. C., 1986. Nouvelles espéces de Chitinozoaires du Pridoli de Libye. *Revue de Micropaléontologie* 29 (1): 44–54.

JARDINÉ, S. & YAPAUDJIAN, L., 1968. Lithostratigraphie et palynologie du Dévonien–Gothlandien gréseux du Bassin de Polignae (Sahara). *Revue de l'Institut Français du Pétrole* 23: 439–455.

JELL, J. S., 1968. New Devonian rock units of the Broken River Embayment, north Queensland. *Proceedings of the Royal Society of Queensland* 87: 63–76.

KENNEY, J. P. L., 1937. Tyers River limestone. *Records of the Geological Survey of Victoria* 1936: 702–707.

LANGE, F. W., 1967. Biostratigraphic subdivision and correlation of the Devonian in the Paranà Basin. *Boletim Paranaense de Geociências* 21/22: 63–98.

LAUFELD, S., 1974. Silurian Chitinozoa from Gotland. *Fossils and Strata* 5: 1–130.

MAGLOIRE, L., 1967. Étude stratigraphique, par la palynologic, des dépôts argilo-gréseux du Silurien et du Dévonien inférieur dans la région du Grand Erg oeeidental (Sahara algérien). In *International Symposium on the Devonian System, Calgary, 1967*, vol. 2, D. H. Oswald, ed., Alberta Soeiety of Petroleum Geologists, Calgary, 473–491.

MASSA, D., & MOREAU-BENOIT, A., 1976. Essai de synthèse stratigraphique et palynologique du système Dévonien en Libye oeeidentale. *Revue de l'Institut Français du Pétrole* 31: 287–333.

MAWSON, R. & TALENT, J. A., in press. Age of an Early Devonian earbonate fan and isolated limestone elasts and megaclasts, east-eentral Vietoria. *Proceedings of the Royal Society of Victoria* 106.

MAWSON, R., TALENT, J. A., BEAR, V. C., BENSON, D. S., BROCK, G. A., FARRELL, J. R., HYLAND, K. A., PYEMONT, B. D., SLOAN, T. R., SORENTINO, L., STEWART, M. J., TROTTER, J. A., WILSON G. A. & SIMPSON, A. G., 1988. Conodont data in relation to resolution of stage and zonal boundaries for the Devonian of Australia. *Canadian Society of Petroleum Geologists Memoir* 16: 1–40.

MAWSON, R., TALENT, J. A., BROCK, G. A. & ENGELBRETSON, M. J., 1992. Conodont data in relation to sequenees about the Pragian–Emsian boundary (Early Devonian) in south-eastern Australia. *Proceedings of the Royal Society of Victoria* 104: 23–56.

PARIS, F., 1976. Les ehitinozoaires. *Mémoires de la Société Géologique et Minéralogique de Bretagne* 19: 93–133.

PARIS, F., 1977. Les ehitinozoaires. In *Stratigraphie et Paléogeographie. Précambrien. Ère Paléozoïque*, C. Pomerol & C. Babin, eds, Doin éditeur, Paris, 121–122.

PARIS, F., 1978. Apports du mieroscope électronique á balayage dans l'étude des ehitinozoaires opaques. *Annales des Mines de Belgique* 1978: 193–202.

PARIS, F., 1979. Biostratigraphie des ehitinozoaires: un exemple dans l'Emsien supérieur armorieain. In *Septième Réunion Annuelle des Sciences de la Terre—Société géologique de France, Lyon 1979*, 353.

PARIS, F., 1980. Les ehitinozoaires. *Mémoires de la Société Géologique et Minéralogique de Bretagne* 23: 52–82.

PARIS, F., 1981a. Les ehitinozoaires dans le Paléozoïque du sud-ouest de l'Europe. *Mémoires de la Société Géologique et Minéralogique de Bretagne* 26: 1–412.

PARIS, F., 1981b. Les ehitinozoaires. *Mémoires de la Société Géologique et Minéralogique de Bretagne* 24: 47–71.

PHILIP, G. M., 1962. The palaeontology and stratigraphy of the Siluro-Devonian sediments of the Tyers area, Gippsland, Vietoria. *Proceedings of the Royal Society of Victoria* 75: 123–246.

PHILIP, G. M., 1965. Lower Devonian eonodonts from the Tyers area, Gippsland, Victoria. *Proceedings of the Royal Society of Victoria* 75: 95–117.

PHILIP, G. M. & PEDDER, A. E. H., 1967. The correlation of some Devonian limestones of New South Wales and Victoria. *Geological Magazine* 104: 232–239.

RAHMANI, K., 1978. Présence de chitinozoaires, d'acritarches et de spores dans le Paléozoïque de la région de Rabat, Maroc. *Palinologia extraordinario* 1: 375–384.

REHFISCH, M. W. & WEBB, J. A., 1993. The Early Devonian Coopers Creek Limestone, a re-deposited deep-water limestone within the Melbourne Trough, southeastern Australia. *Australian Journal of Earth Sciences* (in press).

SORENTINO, L., 1989. Conodont assemblages spanning the Lochkovian–Pragian (Early Devonian) boundary at Eurimbla, central New South Wales. *Courier Forschungsinstitut Senckenberg* 117: 81–117.

SWEET, W., 1985. Conodonts: those fascinating little whatzits. *Journal of Paleontology* 59: 485–494.

TALENT, J. A., MAWSON, R., ANDREW, A. S., HAMILTON, P. J. & WHITFORD, D. J., in press. Middle Palaeozoic extinction events: quest for isotopic signatures: preliminary data. *Palaeogeography, Palaeoclimatology, Palaeoecology.*

TALENT, J. A. & YOLKIN, E. A., 1987. Transgression-regression patterns for the Devonian of Australia and southern west Siberia. *Courier Forschungsinstitut Senckenberg* 92: 235–249.

TAUGOURDEAU, P., 1966. Les chitinozoaires, techniques d'études, morphologie et classification. *Mémoires de la Société Géologique de France* 45: 1–64.

TAUGOURDEAU, P. & DE JEKHOWSKY, P., 1960. Répartition et description de chitinozoaires Siluro-Dévoniens de quelques sondages de la CREPS, de la CFPA, et de la SN REPAL au Sahara. *Revue de l'Institut Français du Pétrole* 15: 1199–1260.

TELFORD, P. G., 1972. Lower and Middle Devonian conodont faunas from the Broken River Embayment, north Queensland. PhD thesis, Department of Geology and Mineralogy, University of Queensland, Brisbane.

TELFORD, P. G., 1975. Lower and Middle Devonian conodonts from the Broken River Embayment, north Queensland, Australia. *Special Papers in Palaeontology* 15: 1–96.

TYSON, R. V. & PEARSON, T. H., 1991. Modern and ancient continental shelf anoxia: an overview. In *Modern and Ancient Shelf Anoxia,* R. V. Tyson & T. H. Pearson, eds, Geological Society of London Special Publication No. 58, 1–24.

URBAN, J. B., 1972. A reexamination of Chitinozoa from the Cedar Valley Formation of Iowa with observations on their morphology and distribution. *Bulletins of American Paleontology* 63 (275): 1–44.

URBAN, J. B. & KLINE, J. K., 1970. Chitinozoa of the Cedar City Formation, Middle Devonian of Missouri. *Journal of Paleontology* 44: 69–76.

URBAN, J. B. & NEWPORT, R. L., 1973. Chitinozoa of the Wapsipinicon Formation (Middle Devonian) of Iowa. *Micropaleontology* 19: 239–346.

VANDENBERG, A. H. M., 1988. Silurian–Middle Devonian. In *Geology of Victoria,* 2nd edn, J. G. Douglas & J. A. Ferguson, eds, Victorian Division, Geological Society of Australia, Melbourne, 103–146.

VOLKHEIMER, W., MELENDI, D. L. & SALAS, A., 1986. Devonian chitinozoans from northwestern Argentina. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 173: 229–251.

WILSON, G. A., 1989. Documentation of conodont assemblages across the Lochkovian–Pragian (Early Devonian) boundary at Wellington, central New South Wales, Australia. *Courier Forschungsinstitut Senkenberg* 117: 117–171.

WINCHESTER-SEETO, T., 1993. Chitinozoa from the Early Devonian (Lochkovian–Pragian) Garra Limestone, central New South Wales, Australia. *Journal of Paleontology* 66: 738–758.

WRONA, R., 1980. Upper Silurian–Lower Devonian Chitinozoa from the subsurface of southeastern Poland. *Palaeontologia Polonica* 41: 103–165.

WYATT, D. H. & JELL, J. S., 1980. Devonian and Carboniferous stratigraphy of the northern Tasman Orogenic Zone in the Townsville hinterland, north Queensland. In *The Geology and Geophysics of Northeastern Australia,* R. A. Henderson & P. J. Stephenson, eds, Geological Society of Australia, Queensland Division, Brisbane, 201–228.

ZIEGLER, W. & LANE, H. R., 1987. Cycles in conodont evolution from Devonian to mid-Carboniferous. In *Palaeobiology of Conodonts,* R. J. Aldridge, ed., British Micropalaeontological Society Series, Chichester, 147–163.

LOWER DEVONIAN (PRAGIAN–EMSIAN) STROMATOPOROIDS FROM VICTORIA

B. D. Webby[1], C. W. Stearn[2] & Y. Y. Zhen[1]

[1]Department of Geology & Geophysics, University of Sydney, New South Wales, 2006
[2]Department of Earth & Planetary Sciences, McGill University, Montreal, H3A 2A7, Canada

Webby, B. D., Stearn, C. W. & Zhen, Y. Y., 1993:11:01. Lower Devonian (Pragian–Emsian) stromatoporoids of Victoria. *Proceedings of the Royal Society of Victoria* 105 (2): 113–185. ISSN 0035-9211.

The Lower Devonian (Pragian–Emsian) stromatoporoid faunas of Victoria are described. The diverse assemblages include much of the material used in the original descriptions of Elizabeth Ripper in the 1930s supplemented by new collections from the most fossiliferous successions. Altogether 37 species represent 23 genera of stromatoporoids. New species are the clathrodictyids *Atelodictyon hicksense* and *Clathrodictyon? heathsense*, the stromatoporellid *Amnestostroma holmesae*, the stromatoporids *Parallelopora ampla, Habrostroma tyersense* and *Columnostroma clathratum*, and the amphiporid *Stellopora porrecta. Plectostroma, Petridiostroma, Stictostroma, Tubuliporella, Syringostromella, Coenostroma* and *Columnostroma* are recorded from Australia for the first time. The microstructures of the best preserved specimens are also described and illustrated.

The assemblages represent three biostratigraphically distinct assemblages: (i) the lower–mid Pragian (*sulcatus* to *kindlei* conodont biozones) association of the Lilydale Limestone at Lilydale and the Coopers Creek Limestone near Tyers, which include key elements such as *Plectostroma altum, Aculatostroma?* sp., *Schistodictyon? cylindriferum, Pseudoactinodictyon* sp., *Atelodictyon chapmani, Stromatoporella* cf. *granulata, Tubuliporella calamosa, Amnestostroma holmesae, Salairella lilydalensis, Syringostromella zintchenkovi, Habrostroma tyersense, Columnostroma clathratum* and *Dendrostroma?* sp.; (ii) the basal Emsian (*dehiscens* conodont Biozone) association in the Buchan Caves Limestone of the Buchan district with restricted elements such as *Clathrodictyon? heathsense, Pseudotrupetostroma buchanense* (and possibly *P. ripperae*), *Syringostromella* cf. *labyrinthea, Coenostroma* sp. and *Atopostroma distans*; and (iii) the lower–mid Emsian (*perbonus* conodont Biozone) association of the upper Murrindal Limestone of the Buchan area with key elements such as *Petridiostroma delicatulum, Pseudotrupetostroma* sp., *Parallelopora ampla* and *Atopostroma* sp.

The biostratigraphically well-constrained Pragian–lower Emsian assemblages of Victoria exhibit many genera, such as *Pseudoactinodictyon, Stromatoporella, Stictostroma, Tubuliporella, Parallelopora, Pseudotrupetostroma* and *Coenostroma*, which are more characteristic of Middle rather than Lower Devonian successions in many parts of Asia, Europe and North America. These occurrences indicate that all these forms have significant Lower Devonian records, at least locally. A brief review of the significant features of the Australian Devonian stromatoporoid faunal record is presented, as well as an outline of the global Lower Devonian succession of stromatoporoid faunas.

STROMATOPOROIDS were first noted as occurring in Siluro-Devonian successions of Victoria by Chapman (1912a, 1912b, 1913, 1914), but it was Elizabeth Ripper who first contributed significantly to the knowledge of the Victorian Devonian assemblages. Her work was published in a series of pioneering papers by the Royal Society of Victoria during the 1930s, based on material from a number of limestone bodies, most notably from Lilydale and Loyola (Fig. 1) in central Victoria (Ripper 1933, 1937a, 1937b), and from the Buchan district of eastern Victoria (Ripper 1937c). She recognized the Lilydale stromatoporoids as including a high percentage of forms characteristic of the Lower

Devonian, a much smaller Loyola assemblage of possibly older (maybe Silurian) elements, and the varied Buchan faunas as having a mainly 'Middle Devonian' aspect (Ripper 1938). She also attempted a full analysis of the evolutionary relationships of the Victorian faunas, especially in the context of other known Silurian and Devonian associations in Europe and North America.

STRATIGRAPHIC SETTING

The Lilydale Limestone was described by Crohn (1953) as a 220 m thick, steeply dipping, lenticular mass within a sequence of interbedded
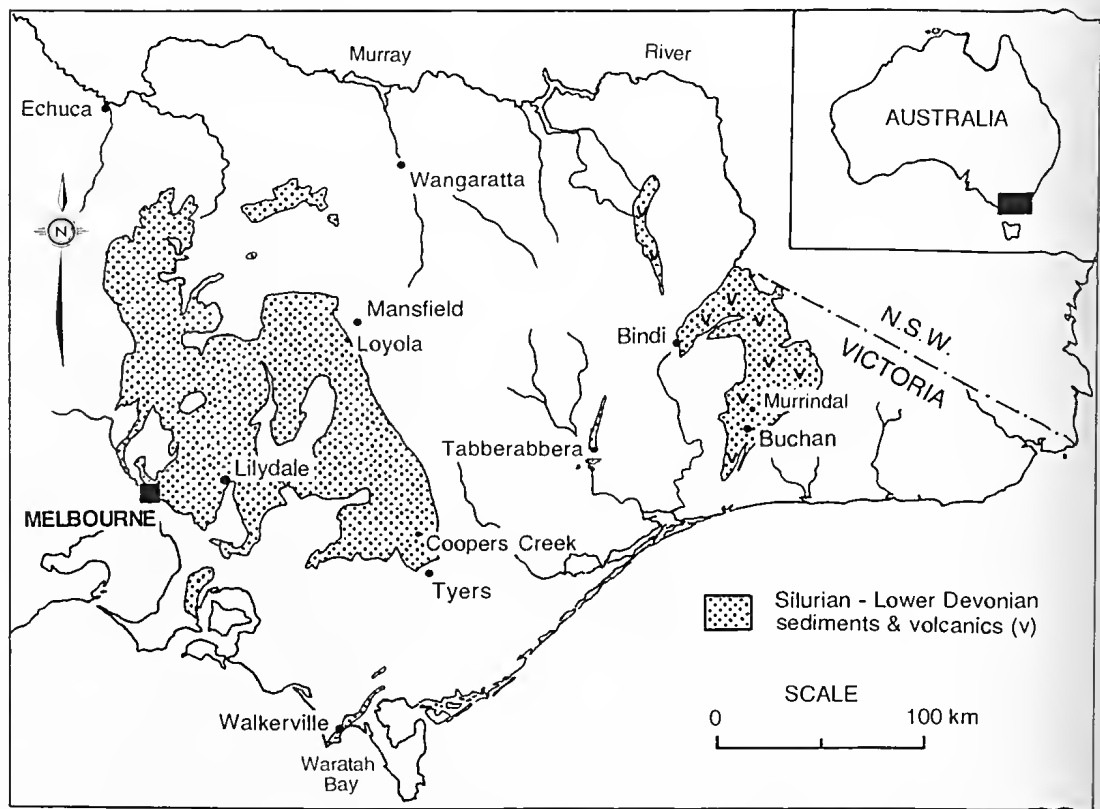
Fig. 1. Map of central and eastern Victoria showing the general outcrop areas of Silurian–Lower Devonian sequences, and the locations of the main Lower Devonian (Pragian–lower Emsian) stromatoporoid-bearing limestones.

shales and sandstones at the Cave Hill quarry site, 1.3 km south-west of Lilydale township. Crohn established its stratigraphic relationships as being underlain, seemingly with conformity, by a great thickness of Humevale Siltstone (= Ruddock Siltstone), and overlain unconformably by a 'quartzite' unit (the Cave Hill Sandstone of VandenBerg 1971). VandenBerg (1971) first considered the Lilydale Limestone to be too limited in extent to warrant formation status. He regarded it as a limestone member in the uppermost part of the Humevale Siltstone. Later, VandenBerg (1975) reinterpreted the limestone body as an allochthonous lens ('a large megaclast') in the shales and included it with the overlying sandstones in a redefined 'conformable' Cave Hill Formation. However, after excavation of the site and exposure of the angular unconformity between the Lilydale Limestone and the overlying Cave Hill Sandstone, VandenBerg (1988: 111) adopted the original interpretation of Crohn (1953).

The very thick (3700 m) succession of Humevale Siltstone underlying the Lilydale Limestone contains four separate brachiopod assemblage zones which apparently span the entire upper Ludlow through Přídolí to Lochkovian interval (Garratt 1983, Garratt & Wright 1988). The diverse Lilydale Limestone faunas (locality 6 of Gill 1940, fig. 1) were listed as including 18 species of stromatoporoids, 9 tabulates, 8 rugosans, a varied gastropod and bivalve fauna and a rich conodont assemblage. VandenBerg (1971) referred to the stromatoporoids as having the appearance of boulders in the detrital-biostromal limestones. The rugose corals were described by Hill (1939). Philip & Pedder (1967) recorded the conodont zonal index *Eognathodus sulcatus*, indicating an early Pragian age (Oliver & Chlupáč 1991) for the Lilydale Limestone (Fig. 2).

The concept of the local Victorian stratigraphic subdivision Yering Series of Gregory (1903), or 'Yeringian', was based on the strata in

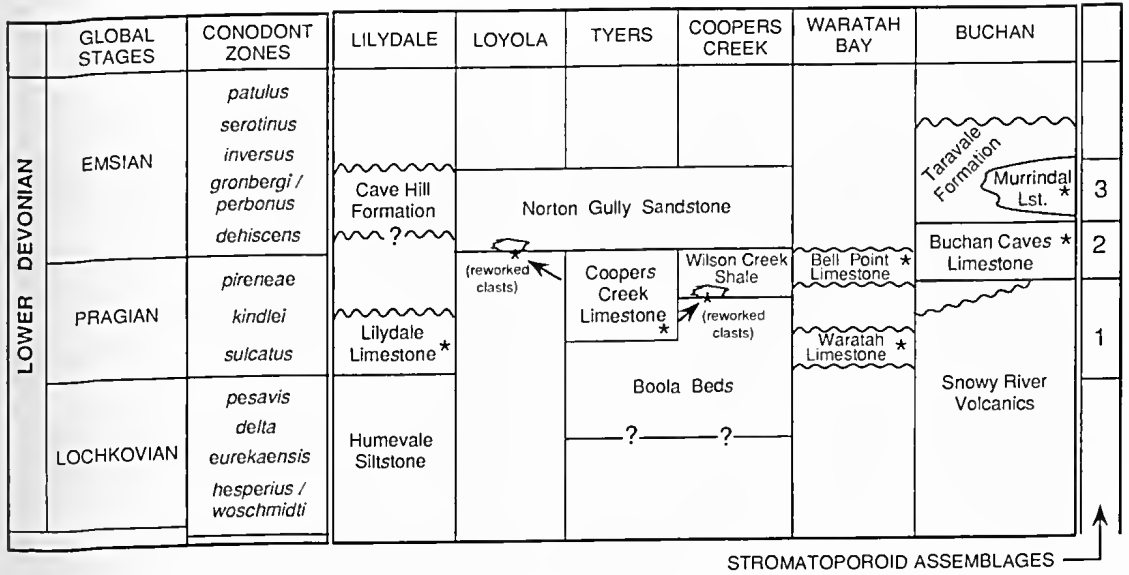|	GLOBAL STAGES	CONODONT ZONES	LILYDALE	LOYOLA	TYERS	COOPERS CREEK	WARATAH BAY	BUCHAN	
LOWER DEVONIAN	EMSIAN	patulus							
		serotinus							
		inversus			Norton Gully Sandstone			Taravale Formation	
		gronbergi / perbonus	Cave Hill Formation					Murrindal Lst. ★	3
		dehiscens	~~ ? ~~			Wilson Creek Shale	Bell Point ★ Limestone	Buchan Caves ★ Limestone	2
	PRAGIAN	pireneae	(reworked clasts)	Coopers Creek Limestone ★		(reworked clasts)			1
		kindlei	Lilydale Limestone ★				Waratah ★ Limestone		
		sulcatus						Snowy River Volcanics	
				Boola Beds					
	LOCHKOVIAN	pesavis	Humevale Siltstone	——— ? ——— ? ———					
		delta							
		eurekaensis							
		hesperius / woschmidti							

STROMATOPOROID ASSEMBLAGES ⟶

Fig. 2. Stratigraphic chart to show the age relations of the main stromatoporoid-bearing units in the Lower Devonian sequences of Victoria (after VandenBerg 1988; Mawson 1987; Mawson et al. 1988, 1992). The main stratigraphically distinct Pragian–lower Emsian assemblages (1–3) are shown in the the right column. Asterisks denote stromatoporoid horizons or occurrences referred to in the text. Arrows suggest possible sources of reworked stromatoporoid-bearing clasts.

the Lilydale district and apparently included most of what is now Humevale Siltstone, Lilydale Limestone and Cave Hill Sandstone. This sequence was viewed until the 1930s as having a Silurian (Wenlock to Ludlow) age, but the palaeontological and stratigraphic work into the 1940s led to reassignment of the whole (Gill 1942), or of the upper part only, to the Lower Devonian (for discussion see Philip 1960). The Yeringian, and names such as the Yering Beds of Gill (1942) and the Yering Group of Talent (1965) and Talent & Banks (1967), this latter comprising the Ruddock Siltstone and the Lilydale Limestone, have fallen into disuse.

When Ripper worked on the faunas of the Lilydale Limestone, however, the term 'Yeringian' was still much used. In her earliest (1933) paper she referred to the Lilydale stromatoporoid occurrences as 'Silurian (Yeringian)', but later (1937c) argued that a higher proportion of the species were more identifiable with the Devonian than with the Silurian, and in her 1938 paper she viewed the 'Yeringian' fauna of Lilydale as characteristic of the Lower Devonian.

Gill's (1942) assignment of the entire 'Yeringian' to the Lower Devonian was too restrictive for, as we now know, the sequence of Humevale Siltstone to Cave Hill Sandstone, inclusive,

spans a very large time interval, comprising much of the Late Silurian (late Ludlow) to Early Devonian (Emsian). Since 1960 the local stage subdivisions for the Silurian and Devonian have progressively been abandoned in favour of using internationally adopted and accepted nomenclature (Talent et al. 1975).

Conaghan et al. (1976: 529) and VandenBerg (1988) referred to the limestones at Loyola, near Mansfield, as allochthonous lenses within the Norton Gully Sandstone (Fig. 2). Conodonts from these bodies include Polygnathus pireneae and Ozarkodina buchanensis, which suggested to Mawson (1987: 284) the kindlei or to Mawson et al. (1988) the pireneae biozones of middle or late Pragian age. The matrix of the Norton Gully Sandstone is regarded by VandenBerg (1988, table 4.1) as younger, equating with the Cave Hill Sandstone and of probable Emsian age. Stromatoporoids have been collected from the limestone lenses exposed at Griffith's Quarry (Ripper 1937a) and Lime Kiln Quarry, Loyola (see map of Cooper 1973, fig. 1).

In the Tyers area, the Lower Devonian sequence includes, in ascending stratigraphic order, the Boola Beds (= Formation), the Coopers Creek Limestone and the sandy Walhalla Beds (Norton Gully Sandstone equivalents). The biotas through the Boola Beds to

Coopers Creek interval are richly diverse and have been documented partly by Philip (1962). A varied coral, stromatoporoid and conodont fauna has been recorded from many localities (and horizons) in the Coopers Creek Limestone, including fossil locality no. 11 of Philip (1962, fig. 1) at Tyers Quarry, the type locality of the conodont *Eognathodus sulcatus* Philip, 1965, which characterises the early Pragian *sulcatus* Biozone, though the section in the quarry extends upwards into the overlying mid-Pragian *kindlei* Biozone (Mawson & Talent in press). Philip (1962) listed a total of 19 stromatoporoid species from various localities (and horizons) in the Cooper Creek Limestone of the Tyers area, some possibly from higher stratigraphic levels, namely within the late Pragian *pireneae* to earliest Emsian *dehiscens* zonal interval (Mawson & Talent in press). However, none of these was described subsequently, and few have been confirmed in existing collections. The present survey focused on stromatoporoids from levels in the upper *sulcatus* to lower *kindlei* interval at Tyers Quarry, and from the Evans Quarry limestone megaclast of *kindlei* age near the former settlement of Coopers Creek (Figs 2–3).

Philip (1960) first recorded occurrences of Devonian stromatoporoids from the Bell Point Limestone at Waratah Bay. The Lower Devonian succession in this area comprises the Waratah Limestone unconformably overlain by the Bell Point Limestone (Talent 1965). The Waratah Limestone contains a moderately varied coral fauna and the conodont *Eognathodus sulcatus* (Fig. 2), suggesting correlation with the Lilydale Limestone and the lower part of the Coopers Creek Limestone (Philip & Pedder 1967, Garratt 1983, Mawson & Talent in press). Mawson et al. (1988: 496) placed almost the entire Waratah Limestone within the *sulcatus* Biozone. The overlying Bell Point Limestone has not yielded diagnostic conodonts though it has a rich macrofauna. Like the Buchan Caves Limestone, it has representatives of the *Spinella–Buchanathyris* brachiopod assemblage zone (Garratt & Wright 1988), probably suggesting correlation with lower Emsian levels. However, it may be better aligned with the lower part of the Buchan Caves Limestone, that is, equating with the late Pragian *pireneae* Biozone (J. A. Talent, pers. comm.). In the present work stromatoporoids have been collected from the Waratah Limestone, and the '*Amphipora*' beds of the Bell Point Limestone has been sampled along the coast near Walkerville (Fig. 3). Philip (1960: 153) listed a number of species additional

to '*Amphipora*' (= *Stellopora*) from the Bell Point Limestone but these have not been verified in our collections or in those of the Museum of Victoria.

In the Buchan area of eastern Victoria, the Buchan Caves Limestone is in excess of 200 m thick and has a mainly sheet-like configuration, though Talent (1988) recorded a coral-stromatoporoid rich buildup in the upper part at Heath's Quarry, and another seemingly low in the formation (J. A. Talent, pers. comm.) at Martin Cameron's Quarry. The Buchan Caves Limestone is succeeded by approximately 700 m of mudstones and nodular limestones of the Taravale Formation, which intertongues into the wedge-shaped body of the Murrindal Limestone, itself up to 250 m thick (Teichert & Talent 1958; Talent 1965, 1969), and with an associated coral–stromatoporoid buildup (a carbonate 'mud-mound') at Rocky Camp between Buchan and Murrindal. These units, together forming the Buchan Group, exhibit a rich and varied biota (Teichert & Talent 1958).

Mawson (1987) established a polygnathid-based conodont zonal succession through these deposits, especially within the Taravale Formation. The lower part of the Buchan Caves Limestone is poorly fossiliferous and dolomitic, with the more diverse faunas limited to the upper part of the formation (Mawson et al. 1992). The Heath's Quarry buildup is considered to have formed in the upper Buchan Caves Limestone. No conodonts have been found in these massive coral–stromatoporoid–'algal' deposits. However, based on conodont data from the immediately overlying Taravale Formation, Mawson et al. (1992: 37) have inferred that construction continued from the time of the *dehiscens* Biozone until about the beginning of the *perbonus* Biozone.

The *perbonus* Biozone is recorded through the middle part of the Taravale Formation and the upper part of the Murrindal Limestone (including the Rocky Camp buildup). The *dehiscens* and *perbonus* biozones approximately span the lower Emsian (or Zlichovian) interval. The *inversus* and *serotinus* biozones have been discriminated in the upper Taravale Formation, but not the uppermost Emsian *patulus* Biozone (Fig. 2).

The stromatoporoids documented by Ripper (1937c) come mainly from two lower Emsian horizons: (1) within the Buchan Caves Limestone (Heath's Quarry, Martin Cameron's Quarry, Citadel Rocks, Murrindal River and probably the locality near Hicks's (now Robert

Global Stages	Pragian						Lower Emsian						
Conodont Zones	*sulcatus*			*kindlei-pireneae*			*dehiscens*						*perbonus*
Formations & Localities / SPECIES	Lilydale Lst. (Lilydale)	Waratah Lst. (Walkerville)	Coopers Creek Lst. (Tyers Quarry)	Lst. megaclast (Evans Quarry)	Loyola Lst. ('Griffith's Ou., ² Lime Kiln Ou.)	Bell Point Lst. (Walkerville)	Heath's Quarry	Martin Cameron's Quarry	Near Hicks'	Citadel Rocks	?Buchan Caves Lst. (Bindi)	Murrindal Limestone (L4 roadside)	Murrindal Lst. (Rocky Camp Quarry)
ACTINOSTROMATIDA													
Actinostroma compactum	X						X	X					X
Actinostroma sp.		X											
Plectostroma altum	X		X										
Aculatostroma? sp.	X	?X											
CLATHRODICTYIDA													
Gerronostroma buchanense							X		X				X
Petridiostroma clarum									X				X
Petridiostroma delicatulum													X
Petridiostroma sp.					X[1]								
Clathrodictyon sp.								X					
Clathrodictyon? heathsense sp. nov.							X		X aff.			X cf.	
Schistodictyon? cylindriferum	X												
Pseudoactinodictyon sp.			X										
Atelodictyon chapmani	X				?X[1]								
Atelodictyon hicksense sp. nov.									X				X
Atelodictyon sp.											X		
STROMATOPORELLIDA													
Stromatoporella cf. *granulata*	X				?X[2]								
Stictostroma sp.												X	X
Tubuliporella calamosa	X												
Dendrostroma? sp.	X												
Amnestostroma holmesae sp. nov.	X		X										
STROMATOPORIDA													
Pseudotrupetostroma ripperae	?X						X						
Pseudotrupetostroma buchanense								X					
Pseudotrupetostroma sp.													X
Salairella lilydalensis	X		X										
Stromatopora aff. *polaris*							X[3]	X	X	X			X
Stromatopora sp.	X												
Syringostromella zintchenkovi	X												
Syringostromella cf. *labyrinthea*							X[3]			X			
Parallelopora ampla sp. nov.							X						X
Coenostroma sp.							X						
Habrostroma tyersense sp. nov.	X	?X	X	?X									
Habrostroma sp.													X
Atopostroma distans							X						
Atopostroma sp.													X
Columnostroma clathratum sp. nov.	X												
AMPHIPORIDA													
Stellopora porrecta sp. nov.					X								

Fig. 3. Distribution of the stromatoporoid occurrences in the Pragian to lower Emsian limestone successions of Victoria. The two localities (Griffith's and Lime Kiln quarries) in the Loyola Limestone have different species denoted by superscripts 1 and 2 respectively. Two of the species listed from the Buchan Caves Limestone at Heath's Quarry occur also in the Buchan Caves Limestone at Citadel Rocks, Murrindal River, and are represented on the Heath's Quarry column by addition of superscript 3. *Clathrodictyon?* aff. *heathsense* occurs near Hicks's and *C.?* cf. *heathsense* at the L4 roadside locality near Murrindal.

McRae's property, see Mawson 1987, text-fig. 5)), of *dehiscens* age; and (2) from the Murrindal Limestone (Rocky Camp Quarry) of *perbonus* age. We have added another locality (L4) from the Murrindal Limestone (latest *dehiscens* or early *perbonus* horizon) on the roadside 1 km south of Murrindal School.

DISTRIBUTION OF STROMATOPOROIDS AND BIOSTRATIGRAPHIC RELATIONSHIPS

The Early Devonian stromatoporoids of central and eastern Victoria belong to three biostratigraphically distinct Pragian–Lower Emsian assemblages (Fig. 2). Stromatoporoid assemblage 1 is best represented by the associations in the Lilydale Limestone and Waratah Limestone, of early Pragian age, and the occurrences in the Coopers Creek Limestone at Tyers Quarry, of early–mid Pragian age. The most diverse association is in the Lilydale Limestone at Lilydale, including *Actinostroma compactum*, *Plectostroma altum*, *Aculatostroma*? sp., *Schistodictyon*? *cylindriferum*, *Atelodictyon chapmani*, *Stromatatoporella*? *granulata*, *Tubuliporella calamosa*, *Dendrostroma*? sp., *Amnestostroma holmesae*, *Salairella lilydalensis*, *Stromatopora* sp., *Syringostromella zintchenkovi*, *Habrostroma tyersense*, *Columnostroma clathratum* and possibly *Pseudotrupetostroma ripperae*. The Waratah Limestone at the old lime kilns site at Walkerville South, on Waratah Bay, has a more restricted fauna comprising *Actinostroma* sp., possibly *Aculatostroma*? sp. and *Habrostroma tyersense*? The Coopers Creek Limestone at Tyers Quarry includes *Plectostroma altum*, *Pseudoactinodictyon* sp., *Amnestostroma holmesae*, *Salairella lilydalensis*, and *Habrostroma tyersense*. The key (restricted) elements of this early–mid Pragian faunal assemblage are indicated by asterisks.

These early–mid Pragian occurrences come from shallow-water carbonates that formed on the eastern (those at Tyers and Waratah Bay) and western (those at Lilydale) flanks of the Melbourne Trough (Garratt 1983, fig. 13), now interpreted as part of the Melbourne–Mathinna terrane of Glen et al. (1992). Significantly, Garratt (1983) regarded the stromatoporoids as members of his shallowest '*Favosites–Stromatopora* Community'.

Additionally, allochthonous limestone deposits on the western flanks of the Melbourne Trough exhibit a few reworked Pragian stromatoporoids, most notably at Coopers Creek and at Loyola (Fig. 1). A limestone megaclast at Evans Quarry near Coopers Creek has yielded *Habrostroma tyersense*? of probable mid-Pragian age, and the allochthonous Loyola Limestone bodies include late Pragian occurrences of *Peridiostroma* sp. and *Atelodictyon chapmani*? (Griffith's Quarry), and *Stromatoporella* cf. *granulata*? (Lime Kiln Quarry).

The Bell Point Limestone at Waratah Bay is possibly of similar late Pragian age and exhibits abundant specimens of the amphiporid *Stellopora porrecta*.

Early Emsian stromatoporoid assemblages are mainly restricted to eastern Victoria, especially in the Buchan Caves Limestone and the overlying Murrindal Limestone of the Buchan area (Figs 2–3). Stromatoporoid assemblage 2 of earliest Emsian (*dehiscens* conodont Biozone) age is best represented in the Heath's Quarry buildup, with *Actinostroma compactum*, *Gerronostroma buchanense*, *Clathrodictyon*? *heathsense*, *Pseudotrupetostroma ripperae*, *Stromatopora* aff. *polaris*, *Syringostromella* cf. *labyrinthea*, *Coenostroma* sp. and *Atopostroma distans*. Slightly modified and less diverse associations are represented at other localities in the Buchan Caves Limestone (see Fig. 2), notably from Martin Cameron's Quarry, from near Hicks's, Murrindal, and at the Citadel Rocks. Another possible Buchan Caves Limestone occurrence is at Bindi, where *Atelodictyon* sp. has been recorded. The restricted elements of this basal Emsian 'Buchan Caves' assemblage are indicated above with asterisks, with the possible addition of *Pseudotrupetostroma buchanense* (recorded only from near Hicks's).

Stromatoporoid assemblage 3 occurs in the overlying Murrindal Limestone, and is of early–middle Emsian (*perbonus* conodont Biozone) age. It is best characterized in the Rocky Camp Quarry exposures of the Buchan area (Fig. 3). *Actinostroma compactum*, *Gerronostroma buchanense*, *Petridiostroma clarum*, *P. delicatulum*, *Atelodictyon hicksense*, *Stictostroma* sp., *Pseudotrupetostroma* sp., *Parallelopora ampla*, *Stromatopora* aff. *polaris*, *Habrostroma* sp. and *Atopostroma* sp. are recorded. Roadside locality 4 near Murrindal School includes *Stictostroma* sp. and *Clathrodictyon*? cf. *heathsense*. Key elements of this fauna are indicated by asterisks.

OTHER SIGNIFICANT AUSTRALIAN DEVONIAN STROMATOPOROID OCCURRENCES

The reworked Early Devonian stromatoporoid fauna from the Jesse Limestone of central New South Wales (Webby & Zhen 1993) includes a number of species common in Victorian successions. For example, *Actinostroma compactum, Pseudotrupetostroma ripperae* and *Atopostroma distans*, constituting about one-quarter of the total Jesse fauna, are also recorded from the Buchan Caves Limestone at Heath's Quarry and assigned a probable *dehiscens* age. This accords with the interpretation of Webby & Zhen (1993) that some of the clasts in the allochthonous Jesse Limestone have an early Emsian (*dehiscens* Biozone) age. However, it is also possible that a few reworked elements may be slightly younger in age; for instance, *Pseudotrupetostroma jessiense*, except for slightly wider spacing of laminae, is closely similar to *P.* sp. from the Murrindal Limestone at Rocky Camp Quarry, of early–mid Emsian (*perbonus* conodont Biozone) age. Few other Lower Devonian stromatoporoid sequences from eastern Australia are as yet adequately enough known to allow close comparisons.

In the Broken River Embayment of north Queensland a remarkably complete sequence of limestones exists through the Late Silurian (Wenlock to Přídolí) to earliest Late Devonian (earliest Frasnian) interval, and within these units there is a remarkably diverse assemblage of stromatoporoids. This large fauna including more than 40 taxa is presently under description. In the Jack Limestone (Graveyard Creek Group), which straddles the Přídolí–Lochkovian boundary, there are representatives of *Ecclimadictyon, Plexodictyon, Schistodictyon, Syringostromella, Clavidictyon* and *Amphipora*. Higher in the succession, probably spanning the Lochkovian–Pragian boundary (*pesavis* to *sulcatus* conodont biozones), is the Martins Well Limestone Member (Shield Creek Formation), with an assemblage including *Labechiella, Cystostroma, Actinostroma compactum, Syringostromella, Atopostroma* cf. *distans, A.* sp., and *Habrostroma*. A gap in the sequence means that the next part of the record is missing, but a very rich assemblage follows in the Lomandra Limestone (lower part of the Broken River Group), of late Emsian to early Eifelian age. This unit includes *Rosenella, Stylostroma, Actinostroma, Gerronostroma, Atelodictyon, Stromato-porella, Pseudoactinodictyon, Simplexodictyon, Pseudotrupetostroma* and *Atopostroma*. The overlying Dosey Limestone spans the upper Eifelian to lower Givetian (*ensensis* conodont Biozone) and contains representatives of *Gerronostroma, Anostylostroma, Parallelopora* and *Salairella*. The Dip Creek Limestone and Chinaman Creek Limestone faunas studied by Mallett (1970a, 1970b, 1971) range from the late Emsian to early Givetian (equivalent to the Lomandra and Dosey Limestones combined) and include similar generic components to those listed above, as well as *Tienodictyon, Hermatostroma, Stictostroma, Stachyodes* and *Stromatopora*. The uppermost unit is the Stanley Limestone Member of the Mytton Formation, of earliest Frasnian age, and it contains *Actinostroma, Anostylostroma, Stachyodes, Salairella* and *Stromatopora*.

Stromatoporoids from the Devonian reef complexes of the Canning Basin, Western Australia, were documented by Cockbain (1984), who described 25 species, principally from the Sadler Limestone (early–mid Frasnian) and the Pillara Limestone (late Givetian–Frasnian). The genera include *Actinostroma, Anostylostroma, Atelodictyon, Clathrocoilona, Stromatoporella, Dendrostroma, Trupetostroma, Pseudoactinodictyon, Hermatostroma, Stromatopora, Stachyodes* and *Amphipora*. A less diverse assemblage (6 species) occurs in coeval shelf deposits of the Carnarvon Basin (Cockbain 1985). Cockbain (1984, 1989) also recorded small Famennian assemblages comprising species of *Clathrocoilina* and *Stromatopora* from the Canning Basin, and *Pennastroma* and *Platiferostroma* from the Bonaparte Gulf Basin.

EARLY DEVONIAN STROMATOPOROID FAUNAL SUCCESSION AND GLOBAL IMPLICATIONS

Stearn (1979) summarized the major patterns of development of Devonian stromatoporoid faunas as comprising an Early Devonian (Lochkovian–Emsian) history with dominance of holdovers from the Ludlow and Přídolí mixed with a few typically new Devonian genera (Fig. 4), an Eifelian–Frasnian maximum diversification of the fauna (about 45% of the total number of species so far described) and, following the latest Frasnian–Famennian decline, a late Famennian fauna dominated by labechiids. The holdovers from the Silurian include *Labechia*,

	LOCHKOVIAN	PRAGIAN	LOWER EMSIAN
Actinostromatida	*Aculatostroma* ⟶ *Araneosustroma* ⟶	*Zeravshanella* ⟶	
Clathrodictyida	*Atelodictyon* ⟶ *Anostylostroma* ⟶ *Belemnostroma* ⟶	*Pseudoactinodictyon* ⟶	
Stromatoporellida		*Stromatoporella* ⟶ *Tubuliporella* ⟶ *?Dendrostroma* ⟶ *Synthetostroma* ⟶	*?Trupetostroma* ⟶ *Stictostroma* ⟶
Stromatoporida	*Pseudotrupetostroma* – *Habrostroma* – – *Columnostroma* ⟶ *Atopostroma* ⟶ *Syringostroma* ⟶	*Salairella* ⟶	*Parallelopora* ⟶ *Coenostroma* ⟶ *Glyptostromoides* ⟶

Fig. 4. Diagram showing the probable first appearances of many of the characteristic Devonian genera in Early Devonian time. The genera range upwards (that is, in the direction of the arrows). The Silurian–Devonian boundary is at the base of the Lochkovian (left margin of Lochkovian box), and the Middle Devonian is above the Emsian (off to the right of the diagram). First appearances of *Pseudotrupetostroma* and *Habrostroma* are uncertain: the former, which is only doubtfully known in the Lochkovian and Pragian, was well represented by early Emsian time; and the latter, depending on how the genus is interpreted, originated either in the Přídolí (latest Silurian), Lochkovian or Pragian.

Actinostroma, Plectostroma, Clathrodictyon, Actinodictyon, Parallelostroma, Gerronostroma, Peridiostroma, Clathrocoilina, Stromatopora, Syringostromella and *Amphipora*, and genera making their first appearance early in the Devonian include *Anostylostroma, Hammatostroma, Atelodictyon, Aculatostroma, Hermatostroma* and *Taleastroma* (Stearn 1979, text-fig. 1). Genera viewed by Stearn (1979: 230) as particularly characteristic of the Eifelian to Frasnian are *Parallelopora, Stromatoporella, Trupetostroma, Anostylostroma, Clathrocoilina, Stachyodes* and *Stictostroma*. Many of these, however, originated earlier, for example in the Early Devonian (*Anostylostroma, Parallelopora, Stromatoporella, Stictostroma*) or even in the Silurian (*Clathrocoilina*).

Lochkovian assemblages

The earliest Devonian (Lochkovian) faunas are best characterized by those described by Stock & Holmes (1986) from Virginia and by Stock (1988, 1991) from New York, and are dominated by Silurian holdovers such as *Plexodictyon, Parallelostroma, Densastroma, Intexodictyon, Actinostromella* and *Plectostroma*. In addition, Stock (1991) assigned two of the dominant New York species to the new genus *Habrostroma*, but Stearn (1993) considered these species to be typical representatives of *Parallelostroma*. Stearn prefers to view *Parallelostroma* as giving rise to *Habrostroma* in the middle part of the Early Devonian, rather than near the beginning of the Devonian.

More diverse Lochkovian (Bursychirmana and Kunjakska horizons) assemblages were described by Lesovaya (1970, 1972, 1982, 1986) from the Zeravshan–Gissarskiy Mountains of southern Tien Shan, Central Asia. A few of the genera are Silurian holdovers (*Plectostroma, Simplexodictyon, Amnestotroma, Clathrostroma, Stromatopora, Parallelostroma, Paramphipora*) but many additional genera (*Aculatostroma, Araneosustroma, Atelodictyon, Pseudotrupetostroma*? and *Shirdagopora*) appear for the first time. In the Sarainaya horizon (earliest Devonian, probably Lochkovian) on the eastern slopes of the Urals, Bogoyavlenskaya (1977) recorded a similar association with *Bullatella* (probably *Actinostroma*), *Coenellostroma* (possibly *Atelodictyon*), *Amnestostroma, Syringostromella, Parallelostroma, Columnostroma* and *Stellopora*, representing a mixture of Silurian holdovers and new genera.

Allochthonous limestones in the Stuart Bay Formation (probably of Lochkovian age) on Bathurst Island, Arctic Canada (Stearn 1990), have produced a mixed assemblage with Silurian holdovers and new, Early Devonian elements. These latter include species of *Atopostroma, Anostylostroma* (*A. laxum*, an early representative of the genus), *Habrostroma, Syringostroma* (a genus which arose from *Parallelostroma*) and *Belemnostroma*.

Pragian assemblages

Only a few described Lower Devonian assemblages have confirmed Pragian ages. One such assemblage, from the Kushnovina horizon in the Zeravshan–Gissarskiy Mountains of Central Asia, contains the 'new' genera *Synthetostroma* and *Zeravshanella* (Lesovaya 1982, 1986). The oldest Chinese stromatoporoid assemblage, from the Yujiang Formation of Guangxi, southern China, is of latest Pragian to early Emsian age and is probably more appropriately considered an early Emsian rather than a Pragian association (see below). It includes *Clathrodictyon, Anostylostroma, Atopostroma* and *Parallelostroma* (Yang & Dong 1979).

The most diverse Pragian stromatoporoid assemblages known are those of Lilydale and Tyers Quarry, Victoria. The assemblages contain Silurian holdovers (*Actinostroma, Plectostroma, Clathrodictyon*?, *Schistodictyon*?, *Amnestostroma, Stromatopora* and *Syringostromella*), other genera possibly derived from the 'new' Lochkovian faunas of Asia and North America (*Aculatostroma*?, *Atelodictyon, Pseudotrupetos-*

troma?, *Columnostroma* and *Habrostroma*), and a number of forms apparently appearing for the first time in the Pragian, at least locally (*Pseudoactinodictyon, Stromatoporella, Tubuliporella, Dendrostroma*? and *Salairella*). *Pseudoactinodictyon* has previously been considered to be restricted to the Middle Devonian (Stearn 1991), and *Salairella* has not been recorded from strata older than Emsian (Stearn 1983). *Dendrostroma* is represented typically as a Middle–Upper Devonian genus (Stearn 1979). First appearances of *Stromatoporella* and *Tubuliporella* include the Victorian species, *Stromatoporella antiqua* Khalfina, 1961 from the Salair region, and species of *Tubuliporella* from the Altai Mountains of south-west Siberia (Khalfina 1968a), all from similar (?Pragian) stratigraphic levels.

Lower Emsian assemblages

A moderately diverse lower Emsian fauna from the Blue Fiord Formation of Arctic Canada has been documented by Stearn (1983). This assemblage has many holdover genera from the Silurian (*Labechia, Gerronostroma, Clathrodictyon, Clathrocoilina, Stromatopora* and *Amphipora*), though actinostromatids are apparently missing. It also exhibits 'new' Devonian genera such as *Atopostroma, Salairella* and *Glyptostromoides*, the latter presumably the earliest record of this genus. Other new genera have been recorded by Stearn & Mehrotra (1970) from the 'Emsian part' of the Ogilvie Formation of the Yukon Territory, Canada, including species of *Anostylostroma, Stictostroma* and ?*Trupetostroma*.

The Victorian (Buchan) lower Emsian assemblages also have Silurian holdover genera (*Actinostroma, Gerronostroma, Petridiostroma, Clathrodictyon, Atelodictyon, Stromatopora, Syringostromella* and *Stellopora*), as well as 'new' genera such as *Stictostroma, Pseudotrupetostroma, Parallelopora, Atopostroma* and *Coenostroma* (also derived from *Parallelostroma*).

Known Chinese lower Emsian assemblages are restricted to the Yujiang Formation (Yang & Dong 1979) of south-central Guangxi (mentioned above) and the Ganxi Formation of northern Sichuan (Wang 1978). Major expansion of the Chinese Devonian stromatoporoids occurred in the late Emsian and is characterized by such diverse assemblages as those in the Guitang Member of the Beiliu Formation of Guangxi (Yang & Dong 1979). Genera present include *Actinostroma, Plectostroma, Cubodic-*

tyon, Gerronostroma, Clathrodictyon, Pseudo-actinodictyon, Stromatoporella, Atelodictyon, ?Atopostroma, Stromatopora, Syringostromella, Salairella, Taleastroma and *Habrostroma*.

Summary remarks

Silurian holdover genera declined in importance through the Early Devonian with such forms as *Densastroma, Actinostromella, Intexodictyon* and *Plexodictyon* disappearing by the beginning of the Pragian. In contrast there was a slow and progressive rise in the diversity of new Devonian genera. Approximately equal numbers of new stromatoporoid genera appeared in each successive age of the Early Devonian. While the Labechiida (l) remained little changed, there were significant changes to diversity within the Actinostromatida (ac), Clathrodictyida (c), Stromatoporellida (sc) and Stromatoporida (so). In the Lochkovian (Fig. 4), based especially on the records in Central Asia (Uzbekistan) and Arctic Canada, the genera *Aculatostroma* (ac), *Araneosustroma* (ac), *Atelodictyon* (c), *Anostylostroma* (c), *Belemnostroma* (c), possibly *Pseudotrupetostroma* (so), possibly *Habrostroma* (so), *Atopostroma* (so), *Columnostroma* (so) and *Syringostroma* (so) appeared. Pragian first appearances, based particularly on the Victorian record, comprise the genera *Pseudoactinodictyon* (c), *Stromatoporella* (se), *Tubuliporella* (se), possible *Dendrostroma* (se), *Habrostroma* (so), *Salairella* (so) and, based on Middle Asian and Chinese occurrences, *Zeravshanella* (ac) and *Synthetostroma* (se). Early Emsian first appearances, judging from the Victorian and Canadian Arctic records, include possibly *Truptetostroma* (se), *Stictostroma* (se), *Pseudotrupetostroma* (so), *Parallelopora* (so), *Coenostroma* (so) and *Glyptostromoides* (so).

Consequently, by the end of the early Emsian (prior to the time of the *serotinus* conodont Biozone) many of the characteristic Middle Devonian genera, such as *Anostylostroma, Stromatoporella, Stictostroma, Parallelopora* and *Syringostroma*, had appeared. Their subsequent diversification, associated with the major Middle Devonian period of reef development, mainly involved expansion of stocks at the species level.

The patterns of development of Lower Devonian stromatoporoid faunas are now well-documented based on assemblages in Central Asia, China and eastern Australia, and suggest a gradual appearance of new Devonian stocks through Lochkovian, Pragian and Emsian time

(Fig. 4), rather than a sudden evolutionary burst of new innovations immediately prior to the major period of active reef growth in the Middle Devonian.

SYSTEMATIC DESCRIPTIONS

Matthews (1973) recommended use of open nomenclature for certain specimens whose identity could not be exactly determined. This practice has been followed herein, including the use of a question mark where generic or specific assignments are not certain. Other attributions include *aff.* for specimens exhibiting affinities close to but not identical with the established species, and *cf.* for specimens showing comparison with the established species.

For localities of specimens, see the following 1:100 000 topographic map sheets: (1) the Lilydale area, see map sheet 7922 Ringwood for Mitchell's (or Cave Hill) Quarry (grid ref. 813533 to 817536); (2) the Buchan area, see map sheet 8522 Orbost for Martin Cameron's Quarry (grid ref. 002431) and Heath's Quarry (grid ref. 034422), and map sheet 8523 Murrindal for Rocky Camp (Commonwealth) Quarry (grid ref. 060528) and the roadside locality (L4) south of Murrindal School (grid ref. 063576); (3) the Tyers–Coopers Creek areas, see map sheet 8121 Moe for Tyers Quarry (grid ref. 495811) and map sheet 8122 Matlock for Evans Quarry, near Coopers Creek (grid ref. 492958); (4) the Wara-

tah Bay area, see map sheet 8020 Wonthaggi for the old lime kilns site at Walkerville South (grid ref. 129983) and the '*Amphipora*' horizon at the mouth of Bluff Creek, near the Bluff, Walkerville (grid ref. 129985); and (5) the Loyola area, see map sheet 8123 Mansfield for the Lime Kiln Quarry (grid ref. 909129) and Griffith's Quarry (grid ref. 904133) south of Mansfield.

Class STROMATOPOROIDEA Nicholson & Murie, 1879

Order ACTINOSTROMATIDA Bogoyavlenskaya, 1969

Family ACTINOSTROMATIDAE Nicholson, 1886b [*nom. correct.* Stechow, 1922, *ex* Actinostromidae Nicholson, 1886b]

Genus **Actinostroma** Nicholson, 1886b

Type species. A. clathratum Nicholson, 1886a.

Actinostroma compactum Ripper, 1933

Figs 5A–F, 7A–C

Actinostroma compactum Ripper 1933: 153, fig. 5A–B.—Ripper 1937c: 15, pl. 2, figs 7–8.—Ripper 1938: 236.—Teichert & Talent 1958: 16, 20.—Flügel & Flügel-Kahler 1968: 81.
cf. *Actinostroma (Actinostroma)* cf. *compactum.*—Flügel 1958a: 55.—Flügel 1958b: 180.
Actinostroma (Actinostroma) compactum.—Flügel 1959: 134.

Material. Holotype (NMV P141959–60, *ex* NMV P13742) and one paratype (NMV P141885–86) as designated by Ripper (1933). Ripper's (1933) other two paratypes (NMV P141989, *ex* NMV P13743; and NMV P142002, *ex* NMV P13744) should be excluded from the species, as this material represents poorly preserved specimens of *Atopostroma*. The holotype and paratype are from the Lilydale Limestone at Mitchell's (Cave Hill) Quarry, Lilydale. Ripper (1937c) also figured NMV P141806–07 (*ex* MUGD 1617) from Heath's Quarry, Buchan Caves Limestone, near Buchan. Ten other specimens come from the Buchan Caves Limestone at Heath's Quarry (NMV P136228–29, P136230–32, P136233–34, P141761–62, P141791–92, P141802–03, P141789–90, P141794–95, P141804–05), and one specimen from Martin Cameron's Quarry (NMV P136235–36), also near Buchan. In addition, the species is recorded from the Murrindal Limestone at Rocky Camp Quarry near Buchan: three specimens (NMV P136237–38, P136239–40, and P141694).

Description. External details of this species remain uncertain, though a few recently collected specimens show a laminar to low domical external form. Latilaminae conspicuous, and usually 2 to 8 mm thick, but in extremes may be as little as 1.0 mm to more than 15 mm thick. Many specimens exhibit scattered, large, rounded spar-filled cavities up to 1 mm in height and 1.5 mm in width, possibly repesenting a symbiotic organism such as *Topsentopsis* de Laubenfels, 1955. In one thin section (NMV P141802) an irregular basal phase has formed where it grew in competition for available space with a species of *Stromatopora*. A few specimens have broadly undulating laminae, 9 to 14 mm from crest to crest; and these may or may not show associated astrorhizal clusters.

In vertical sections pillars are moderately continuous, traceable for up to 5 mm vertically; confined to latilaminae and interrupted by thickened and relatively disordered phases at the bases of successive latilaminae; this thickened, irregular basal zone may be up to 1 mm thick; pillars from 9 to 12 in 2 mm, and individually 0.04 to 0.10 (typically 0.07) mm in diameter. Laminae usually relatively evenly spaced and continuous, though at a few levels more undulating and laterally discontinuous; individually they may be traced for up to 14 mm laterally; spaced from 10 to 14 in 2 mm vertically, and with rod-like colliculi of each lamina varying from 0.03 to 0.07 (on average 0.05) mm in diameter.

In tangential sections pillars cut as rounded dots, from 0.04 to 0.10 (on average 0.07) mm across, locally with diagenetically replaced centres, and spaced from 0.1 to 0.2 mm apart (with usually 25 to 30 counted in 1 mm^2); hexactinellid networks develop from three to five finer colliculi intersecting each pillar. Astrorhizal canals are most conspicuous in tangential sections, forming parts of an irregularly radiating and branching, stellate structure; these clusters may be large, up to 9 mm across, and may be spaced from between 4 and 12 mm apart through the skeleton; and they only rarely appear to be superposed (NMV P141791); in the periaxial parts of the cluster, individual branching, astrorhizal canals up to 0.25 mm wide (usually 0.15–0.25 mm) occur, but towards the axis of the stellate cluster (within 0.5 mm of the axis), a finer meshwork of vertical pillar-like and horizontal rod-like processes may be seen (NMV P141762); the astrorhizal canals are wall-less (only bounded in places by an alignment of adjacent colliculi). Microstructure in better preserved material is compact.

Remarks. Preservation of the material from the Lilydale and Buchan localities is somewhat variable; the best preserved specimens come from Heath's Quarry in the Buchan Caves Limestone,
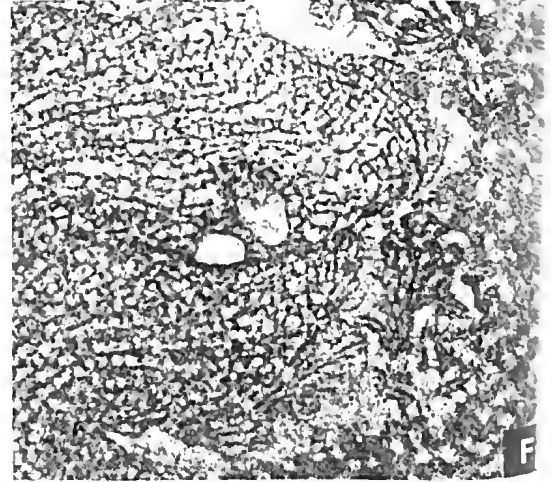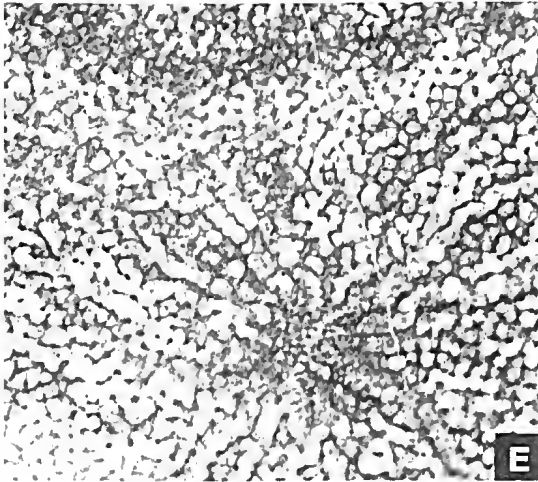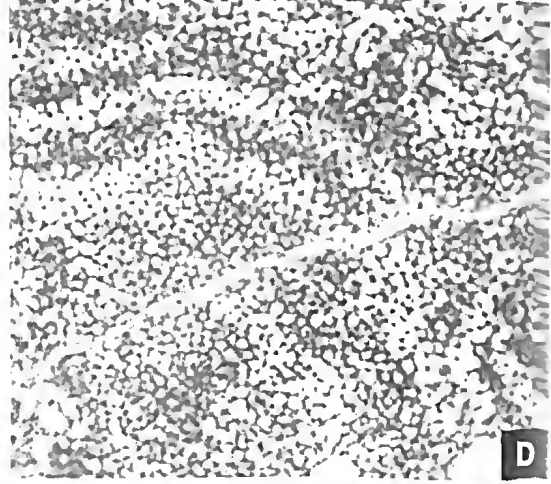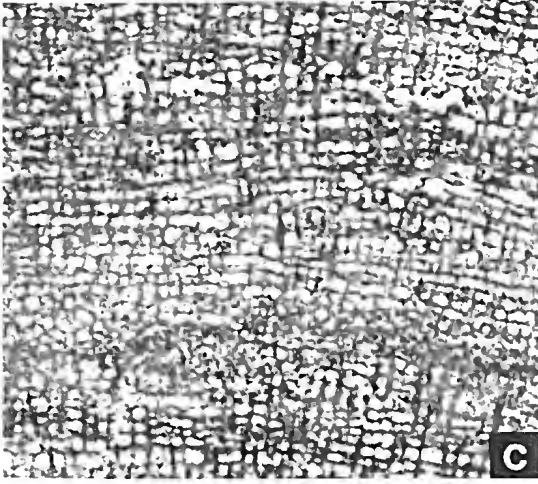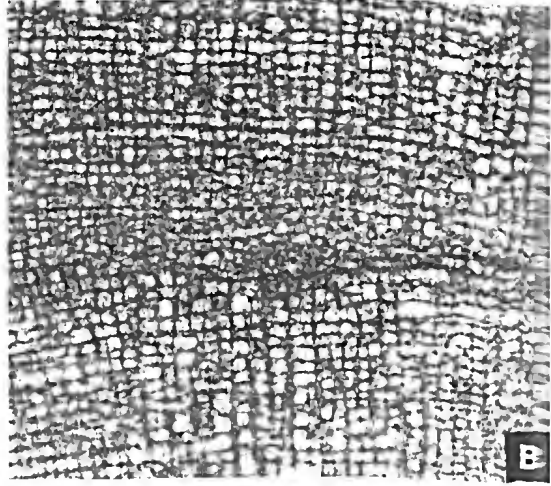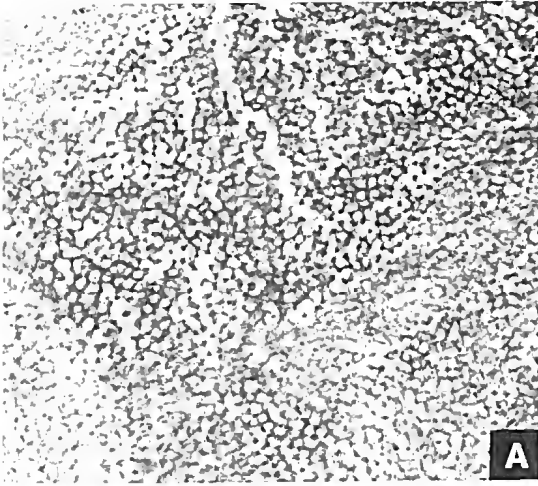
and from the Rocky Camp Quarry in the Murrindal Limestone. The skeletal material of some specimens from Lilydale and from the Buchan Caves Limestone is markedly thickened. In contrast, most of the forms from the Rocky Camp locality have pillars and colliculi with a similar spacing to the other stratigraphically lower, Buchan Caves Limestone representatives, but the elements are somewhat more delicate (?less thickened). However, no sharp line can be drawn between the specimens of these stratigraphically distinct levels. A distinction may also be suggested between the sheet-like, narrowly latilaminate, and the mammillate (often with astrorhizal clusters), more widely latilaminate forms in the assemblages, but again there are gradations between these two groups at both the Lilydale and the Buchan localities. Consequently a broad conception of the species is maintained.

Ripper (1933, 1937c) drew attention to the close relationship between this species and the type species, *Actinostroma clathratum*, and this relationship was confirmed by Flügel (1959). The main differences were given by Ripper as 'the closer crowding' of pillars and laminae of the Victorian species, and the 'fairly regular doming' of laminae to form mamelons. Flügel (1959) added that *A. compactum* occupied an intermediate position morphologically between the coarser *A. clathratum* and the finer *A. stellulatum* Nicholson, 1886a. Material from the allochthonous Early Devonian (Emsian) Jesse Limestone of the Limekilns area, central New South Wales, include representatives of all three morphologies (see Webby & Zhen 1993, and Fig. 6 herein). Specimens of the Pragian *A. compactum* from the type locality at Lilydale are shown in Fig. 6 to occupy an intermediate position between the slightly younger (Emsian) and more variable material (grouped in three species) from the Jesse Limestone. It should be noted that *A. clathratum* and *A. stellulatum* are characteristically Middle and early Late Devonian species in Europe and Asia (Flügel 1959), but that the occurrences in New South Wales are of Emsian age.
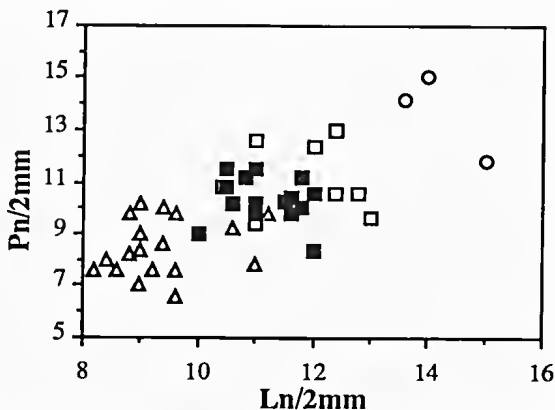
Ripper (1933) assigned two Lilydale speci-

Fig. 6. Scatter diagram of number of pillars and number of laminae in 2 mm to show the range of variability in the species of *Actinostroma* from the Jesse Limestone of the Limekilns area, central New South Wales (Webby & Zhen 1993), and the Lilydale Limestone at Lilydale, central Victoria. Key to symbols: open triangles, *A. clathratum* (Limekilns); solid squares, *A. compactum* including type specimens (Lilydale); open squares, *A. compactum* (Limekilns); and open circles, *A. aff. stellulatum* (Limekilns).

mens to *Actinostroma verrucosum* (Goldfuss, 1826). Only the figured specimen is presently available for study in the collections of the Museum of Victoria (NMV P141889–90, *ex* MUGD 1446); the other is missing. This is a strongly mammillate form with well developed vertical astrorhizal canals centred within the mamelon columns. The mamelons are spaced from 5 to 8 mm apart, and the astrorhizal canals are wall-less structures up to 0.5 mm in diameter. Pillars are of similar dimensions and arrangement to those of *A. compactum*, spaced from 8 to 10 in 2 mm. Laminae are continuous and formed of regularly spaced colliculi in parts of the skeleton, but also show alternations between these open, regularly spaced laminae and closely-spaced, clustered, slightly imbricate rows of small globose elements suggestive of dissepiments; these alternating patterns suggest fluctuating rates of growth. Clearly more material must be found to confirm the presence of *A. verrucosum* in Victoria.

Fig. 5. *Actinostroma compactum* Ripper, 1933, × 10; A, NMV P141807 (*ex* MUGD 1617), tangential section; B, NMV P141806 (*ex* MUGD 1617), vertical section; C, paratype NMV P141885, vertical section; D, holotype NMV P141959 (*ex* NMV P13742), tangential section; E, NMV P141762, tangential section; F, NMV P141803, vertical section showing intergrowth with *Stromatopora* aff. *polaris* (Stearn, 1983) and development of basal phase in the contact zone between them. A, B, E, F from Buchan Caves Limestone at Heath's Quarry; C, D from Lilydale Limestone at Cave Hill Quarry.

The collections include one additional specimen, not referrable to *A. compactum*, from the Waratah Limestone of the old lime kilns site at Walkerville South (NMV P136400–41, *ex* NMV P136213). The specimen, here informally assigned to *Actinostroma* sp., is perhaps allied to *A. stellulatum* but differs from that species in having relatively thicker pillars, 0.1 mm in diameter (Fig. 7D). These pillars appear to have hollow centres, possibly as a result of diagenetic alteration. The laminae are continuous, closely and evenly spaced, from 15 to 20 in 2 mm.

Genus **Plectostroma** Nestor, 1964

Type species. Actinostroma intertextum Nicholson, 1886a.

Remarks. Flügel (1959) included three Devonian species (*A. salairicum* Yavorsky, 1930, *A. altum* Ripper, 1933 and *A. ligeriense* Le Maître, 1934) in the species group of *Actinostroma intertextum*, now attributed to *Plectostroma*. Nestor (1964) and Mori (1969) noted that the radial processes (colliculi) of *Plectostroma* are developed at different levels, not consistently at the same levels as in the regular net-like laminae of *Actinostroma*.

Plectostroma altum (Ripper, 1933)

Figs 7E–F, 8A–D

Actinostroma altum Ripper 1933: 156, figs 2, 5E–F.—
   Philip 1960: 151.—Flügel & Flügel-Kahler 1968:
   22.
Actinostroma (Actinostroma) altum.—Flügel 1959:
   125.

Material. Holotype (NMV P141894–95, P141951–53; *ex* NMV P13745) and topotype (NMV P141903–05, P141941–43; *ex* NMV P13761) from the Lilydale Limestone, Mitchell's (Cave Hill) Quarry, Lilydale. Fig. 2 of Ripper (1933) is drawn from holotype, NMV P141895; fig. 5E is from NMV P141952; and fig. 5F is from NMV P141951. An additional, well preserved specimen (NMV P136241–42, *ex* NMV P136149) comes from the Coopers Creek Limestone at Tyers Quarry.

Description. Skeleton apparently laminar to domical, exhibiting latilaminae from 2 to 8 mm thick. In vertical sections composed of somewhat disordered meshwork of vertical pillars and laminae with irregularly offset, rod-like, colliculi. Pillars are thin, usually continuous through several laminae, observed to extend for up to 2 (in extremes to 4) mm vertically; may be sinuous (possibly in part associated with branching) and commonly scattered throughout the skeleton; 7–10 pillars in 2 mm; individual width from 0.045 to 0.1 mm.

Laminae somewhat undulating, thin but may be variably thickened, and may form a part of laterally continous or more irregularly discontinous tissue; rod-like colliculi of the laminae may intersect pillars at the same level, or at different levels; in some places these latter structures appear as isolated or aligned rows of rounded dots within gallery spaces in vertical sections; laminae spaced from 8 to 10 in 2 mm; individual laminae from 0.02 to 0.08 mm thick. Scattered, variable-sized, upwardly domed-shaped dissepiments may occur through the skeleton, and also much smaller, vertical and horizontal, tube-like astrorhizae, from 0.2 to 0.3 mm wide. Large and small (?worm) tubes may also be associated, the former being up to 1.8 mm across and 1.2 mm in height, and the latter from 0.2 to 0.3 mm across. Thickened zones of horizontal and vertical structural elements define the boundaries between latilaminae. Microstructure is apparently compact.

In tangential sections the pillars appear as rounded dots and tend to be slightly thicker than connecting colliculi; well-developed hexactinellid network is only shown in scattered areas of the skeleton; pillars are from 0.05 to 0.1 mm in diameter, and spaced from 0.1 to 0.2 mm apart; about 16 to 30 pillars spaced within 1 mm^2. Astrorhizae incompletely radiating.

Remarks. Ripper (1933) emphasized the close relationship of this Victorian species to *P. intertextum*. However, she seems to have mistakenly interpreted all the upwardly curved lateral structures of *P. altum* as laminae, though some of these, from tangential-oblique sections, can clearly be seen to be curved dissepimental plates. Furthermore, though she doubted that astrorhi-

---

Fig. 7. A–C, *Actinostroma compactum* Ripper, 1933, × 10; A, NMV P136237 (*ex* NMV P136147), vertical section; B, NMV P136238 (*ex* NMV P136147), tangential section; A, B, Murrindal Limestone, Rocky Camp Quarry; C, NMV P141791, vertical–oblique section, Buchan Caves Limestone, Heath's Quarry. D, *Actinostroma* sp., NMV P136400 (*ex* NMV P136213), vertical section, × 10, Waratah Limestone, limekilns site, Walkerville South. E, F, *Plectostroma altum* (Ripper, 1933), × 10, Lilydale Limestone, Mitchell's (Cave Hill) Quarry; E, holotype NMV P141952 (*ex* NMV P13745), tangential section; F, holotype NMV P141951 (*ex* NMV P13745), vertical section.

CORRIGENDUM

The accompanying sheet replaces pages 127 and 128
of Proceedings of The Royal Society of Victoria,
Vol. 105, No. 2.
As originally issued, page 128 of that number
contained a printing error.

zae were present in *P. altum*, they are plainly visible as incompletely developed, radiating astrorhizal canals in tangential sections of the holotype. *P. intertextum* has closer-spaced laminae (7–12 per mm) and pillars (5–9 per mm), and the astrorhizae are finer (0.09–0.19 mm), according to C. W. Stock (pers. comm.).

From the two other known Devonian species of *Plectostroma*, *P. salairicum* (Yavorsky, 1930) from the Kuznetsk Basin of Siberia, and *P. ligeriense* (Le Maître, 1934) from the Ancenies Basin of France, *P. altum* differs in exhibiting better defined latilaminae, as well as differing from the former in having slightly more widely spaced laminae and from the latter bFAGERSTROM J. A., 1982. Stromatoporoids of the ideyakh *Institut Royal des* LESOVAYA, A. I., 1982. Ranne- i srednedevnskie strohe Royal Society of Victoria 106.

renclature and Mehotra, P. N., 1970. Lower and 2.

Type species. Syringostroma verrucosum Khalfina, 1961.

Aculatostroma? sp.

Fig. 8E–F

Syringostroma densum.—Ripper 1937a: 182, pl. 8, figs 3–5.—Ripper 1938: 236.

Material. One specimen (NMV P141877–80, *ex* MUGD 1620) from the Lilydale Limestone at Mitchell's (Cave Hill) Quarry, Lilydale. Another specimen (NMV P136398–99, *ex* NMV P136227) from the Waratah Limestone at the old lime kilns site at Walkerville South is doubtfully assigned.

Comparative description. Ripper (1937a) noted that this specimen was nearly identical with the type species of *Syringostroma*, *S. densum* Nicholson, 1875 from the Columbus Limestone of Ohio. However it does not show the distinctive larger set of pillars, now known as "megapillars' (Fagerstrom 1982), which in part characterizes the genus. The clinoreticulate megapillars, the diffuse nature of the skeletal material and the prominent microlaminae are taken as typical features of *Syringostroma*.
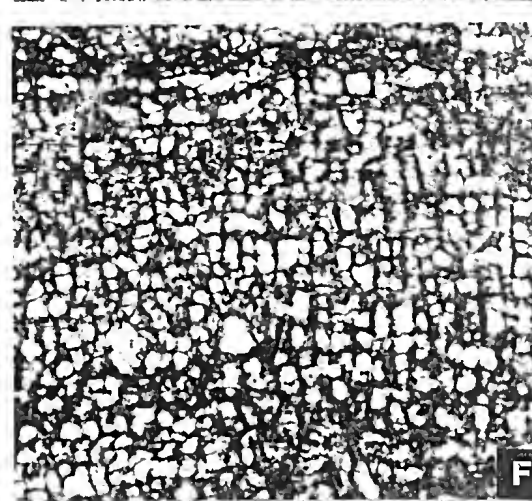
Ripper (1937a) provided a good description

of the Lilydale specimen, featuring its well defined latilaminae from 2 to 5 mm thick (commonly differentiated with a basal thickened zone from 0.7 to 0.9 mm thick), and its irregularly reticulated meshwork comprising slender pillars, up to 0.1 mm in diameter and commonly short, in places superposed but seldom through more than a few interlaminar spaces. She recorded colliculi intersecting the pillars at irregular intervals, and also, at other levels, colliculi coalescing to form laminae, commonly spaced about 5 to 6 in 2 mm and typically at levels where the pillars are interrupted. Astrorhizae are commonly associated with the thickened basal parts of the latilaminae, although a few that are parallel to growth and oblique to vertical canals may also occur more randomly through the rest of the skeleton; they are mainly up to 0.3 mm in diameter.

In tangential section through an interlaminar space, the pillars are round to vermiform with few being interconnected by colliculi, but where the laminae are intersected a fine-textured, closed mesh of comparatively dense, thickened structural elements (pillars and colliculi) is shown; the 'pores' in the laminae are typically rounded and about 0.1 mm in diameter. Astrorhizae are large with six or more radiating and branching canals, up to 0.4 mm across, extending from centres. Under magnification the pillars in tangential section show a very fine speckled, apparently cellular skeletal material; the cellules are 0.01 to close to 0.02 mm across.

The Lilydale specimen shows laminae as a network of colliculi arising from upwardly dividing pillars but is not closely similar to other species of *Aculatostroma* (Stearn 1991). It has some resemblance to *A. ordinatum* (Stearn, 1961) from the Cairn Formation (Middle or Upper Devonian) of Alberta but differs in exhibiting a clustering of astrorhizae near the bottoms rather than the tops of latilaminae. It is therefore left in open nomenclature.

The Waratah specimen has a less densely, thickened meshwork in tangential section and is therefore also doubtfully assigned to *Aculatostroma*.

Fig. 8. A–D, *Plectostroma altum* (Ripper, 1933), × 10; A, topotype NMV P141903 (*ex* NMV P13761), vertical section; B, holotype NMV P141951 (*ex* NMV P13745), vertical section; C, NMV P136241 (*ex* NMV P136149), vertical section; D, NMV P136242 (*ex* NMV P136149), tangential section. E, F, *Aculatostroma*? sp., × 10; E, NMV P141878 (*ex* MUGD 1620), vertical section; F, NMV P141877 (*ex* MUGD 1620), tangential section. A, B, E, F, Lilydale Limestone at Mitchell's (Cave Hill) Quarry; C, D, Coopers Creek Limestone, Tyers Quarry.

zae were present in *P. altum*, they are plainly visible as incompletely developed, radiating astrorhizal canals in tangential sections of the holotype. *P. intertextum* has closer-spaced laminae (7–12 per mm) and pillars (5–9 per mm), and the astrorhizae are finer (0.09–0.19 mm), according to C. W. Stock (pers. comm.).

From the two other known Devonian species of *Plectostroma*, *P. salairicum* (Yavorsky, 1930) from the Kuznetsk Basin of Siberia, and *P. ligeriense* (Le Maître, 1934) from the Ancenies Basin of France, *P. altum* differs in exhibiting better defined latilaminae, as well as differing from the former in having slightly more widely spaced laminae and from the latter bFAGERSTROM J. A., 1982. Stromatoporoids of the ideyakh *Institut Royal des* LESOVAYA, A. I., 1982. Ranne- i srednedevnskie strohe Royal Society of Victoria 106.

renclature and Mehotra, P. N., 1970. Lower and 2.

Type species. Syringostroma verrucosum Khalfina, 1961.

Aculatostroma? sp.

Fig. 8E–F

Syringostroma densum.—Ripper 1937a: 182, pl. 8, figs 3–5.—Ripper 1938: 236.

Material. One specimen (NMV P141877–80, *ex* MUGD 1620) from the Lilydale Limestone at Mitchell's (Cave Hill) Quarry, Lilydale. Another specimen (NMV P136398–99, *ex* NMV P136227) from the Waratah Limestone at the old lime kilns site at Walkerville South is doubtfully assigned.

Comparative description. Ripper (1937a) noted that this specimen was nearly identical with the type species of *Syringostroma, S. densum* Nicholson, 1875 from the Columbus Limestone of Ohio. However it does not show the distinctive larger set of pillars, now known as "megapillars' (Fagerstrom 1982), which in part characterizes the genus. The clinoreticulate megapillars, the diffuse nature of the skeletal material and the prominent microlaminae are taken as typical features of *Syringostroma*.
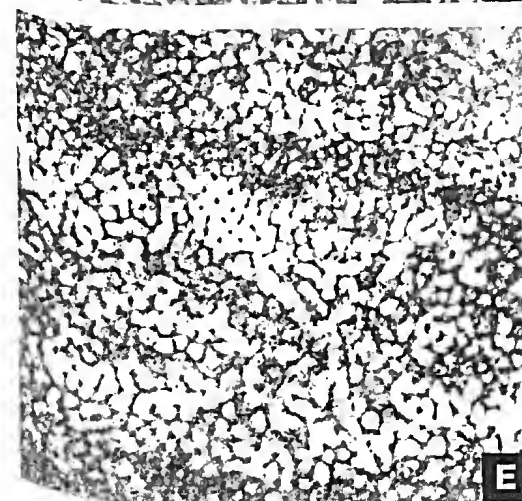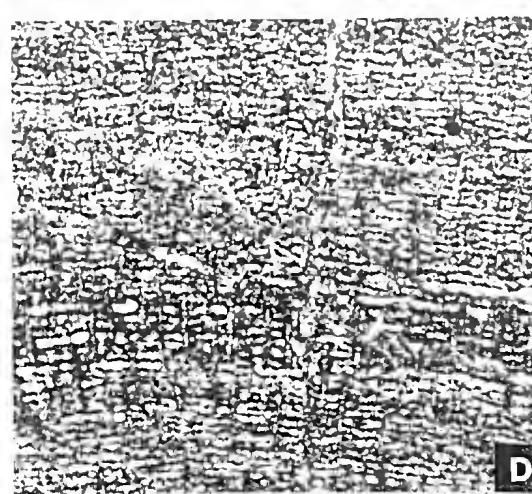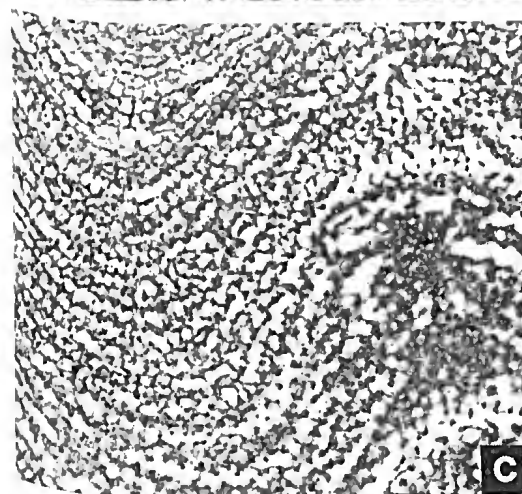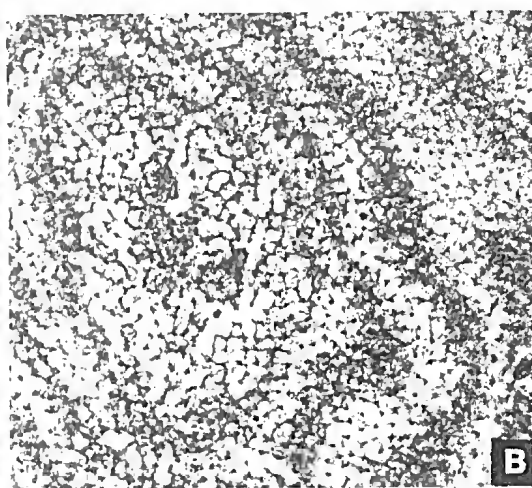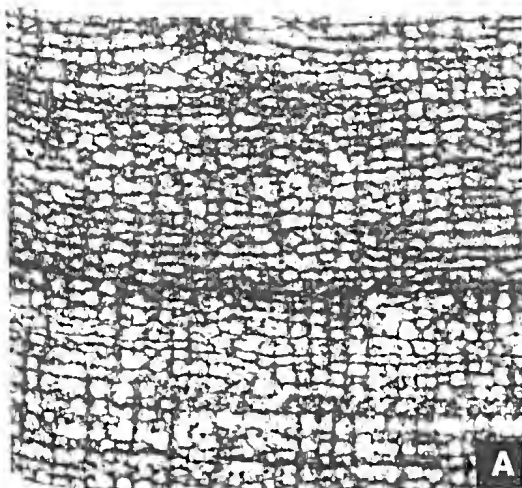
Ripper (1937a) provided a good description of the Lilydale specimen, featuring its well defined latilaminae from 2 to 5 mm thick (commonly differentiated with a basal thickened zone from 0.7 to 0.9 mm thick), and its irregularly reticulated meshwork comprising slender pillars, up to 0.1 mm in diameter and commonly short, in places superposed but seldom through more than a few interlaminar spaces. She recorded colliculi intersecting the pillars at irregular intervals, and also, at other levels, colliculi coalescing to form laminae, commonly spaced about 5 to 6 in 2 mm and typically at levels where the pillars are interrupted. Astrorhizae are commonly associated with the thickened basal parts of the latilaminae, although a few that are parallel to growth and oblique to vertical canals may also occur more randomly through the rest of the skeleton; they are mainly up to 0.3 mm in diameter.

In tangential section through an interlaminar space, the pillars are round to vermiform with few being interconnected by colliculi, but where the laminae are intersected a fine-textured, closed mesh of comparatively dense, thickened structural elements (pillars and colliculi) is shown; the 'pores' in the laminae are typically rounded and about 0.1 mm in diameter. Astrorhizae are large with six or more radiating and branching canals, up to 0.4 mm across, extending from centres. Under magnification the pillars in tangential section show a very fine speckled, apparently cellular skeletal material; the cellules are 0.01 to close to 0.02 mm across.

The Lilydale specimen shows laminae as a network of colliculi arising from upwardly dividing pillars but is not closely similar to other species of *Aculatostroma* (Stearn 1991). It has some resemblance to *A. ordinatum* (Stearn, 1961) from the Cairn Formation (Middle or Upper Devonian) of Alberta but differs in exhibiting a clustering of astrorhizae near the bottoms rather than the tops of latilaminae. It is therefore left in open nomenclature.

The Waratah specimen has a less densely, thickened meshwork in tangential section and is therefore also doubtfully assigned to *Aculatostroma*.

Fig. 8. A–D, *Plectostroma altum* (Ripper, 1933), × 10; A, topotype NMV P141903 (*ex* NMV P13761), vertical section; B, holotype NMV P141951 (*ex* NMV P13745), vertical section; C, NMV P136241 (*ex* NMV P136149), vertical section; D, NMV P136242 (*ex* NMV P136149), tangential section. E, F, *Aculatostroma*? sp., × 10; E, NMV P141878 (*ex* MUGD 1620), vertical section; F, NMV P141877 (*ex* MUGD 1620), tangential section. A, B, E, F, Lilydale Limestone at Mitchell's (Cave Hill) Quarry; C, D, Coopers Creek Limestone, Tyers Quarry.

Order CLATHRODICTYIDA Bogoyavlenskaya, 1969

Family CLATHRODICTYIDAE Kühn, 1927

Genus **Gerronostroma** Yavorsky, 1931

Type species. G. elegans Yavorsky, 1931.

Gerronostroma buchanense (Flügel, 1959)

Fig. 9A–D

non *Actinostroma contortum* Gorsky 1935: 10, 88, pl. 1, figs 1–4.
Actinostroma contortum.—Ripper 1937c: 14, pl. 2, figs 3–6.—Ripper 1938: 236.—Galloway & St Jean 1957: 237.—Teichert & Talent 1958: 16, 20.— Flügel & Flügel-Kahler 1968: 101.
Actinostroma (Actinostroma) buchanense Flügel 1959: 183, pl. 7, fig. 4.
Actinostroma buchanense.—Flügel & Flügel-Kahler 1968: 52.

Material. Holotype (NMV P141758, *ex* MUGD 1611) is from the Buchan Caves Limestone at Heath's Quarry, near Buchan. One other specimen (NMV P141749–50) from the type locality is also assigned to the species, and several specimens from the Murrindal Limestone at Rocky Camp Quarry near Buchan, including Ripper's (1937c) figured specimen (NMV P141690–91, *ex* MUGD 1604), and other specimens (NMV P136243–44, P136245–46, P136247–48, P136249–50, P136251–52, P13653–54, P136255–56, P141692–93, P141700–01, P141707–08, P141713–14, P141716–18, P141729 and P141733).

Description. Skeleton apparently low domical to massive with the growth surface commonly rising into low domal mamelons, spaced from 3.5 to 8 mm between crests, and of moderate relief, from 1.5 to 4 mm in height. Growth interruption surfaces occur in a few places, as well as phases of more closely-spaced laminae, this latter perhaps suggesting a slower growth between successive latilaminae; these phases are spaced from 2 to 3 mm apart. Astrorhizae are well developed within mamelon columns; the complexly partitioned vertical canals are from 0.35 to 1.5 mm in diameter.

In vertical sections, laminae are thin (0.025–0.05 mm), continuous, broadly flexuous, and somewhat irregularly spaced; apparently composed of a single layer of compact skeletal material, and spaced from 7 to 15 (usually 10–12) in 2 mm. In places, especially towards upper flanks and crest of mamelon columns, laminae are closely spaced and intermittently come in contact with neighbours; locally, particularly in troughs between mamelon columns, such laminae are difficult to distinguish from broadly flexuous, long, low dissepiments; a few other distinctive, vesicular-type dissepiments also occur in parts of the skeleton, especially in areas where laminae are widely spaced.

Pillars are distributed randomly, in places long and regularly superposed through at least 10 laminae, and in other places confined to one or two interlaminar spaces; from 0.05 to 0.1 mm in diameter and spaced from 10 to 13 in 2 mm. They are not markedly spool-shaped but a few are wider at the top. Only in a few areas just above growth interruption surfaces is pillar structure disordered and irregular.

In tangential sections, laminae form dense concentric bands with irregular, diffused margins; pillars are visible mainly as discrete rounded dots, approximately 30 per mm^2; a few may be fused to neighours in aligned rows but do not form conspicuous meshworks with adjacent laminae. Astrorhizae are conspicuously developed in the centres of mamelon columns and, although they may show incomplete radiating 'septa-like' partitions in some areas, the main passageway still appears to be open at the axis; however, in vertical sections the large astrorhizae are divided by a series of apparently complete, blister-like astrorhizal tabulae to form a more or less superposed vertical row of partitioned segments, with offsets at various levels of radiating canals (0.25–0.3 mm in diameter) extending into adjacent interlaminar spaces; these canals are also divided by tabulae.

Remarks. This species was originally described as *A. contortum* Ripper, 1937c but was renamed by Flügel (1959) to avoid homonymy with *A. contortum* Gorsky, 1935. Stearn (1966: 101) noted that it would be better placed in *Gerronostroma.* Species of this genus are recorded from the Ludlow to the Frasnian (Flügel & Flügel-Kahler 1968).

Fig. 9. A–D, *Gerronostroma buchanense* (Flügel, 1959), × 10; A, holotype NMV P141758 (*ex* MUGD 1611), vertical section, Buchan Caves Limestone, Heath's Quarry; B, NMV P136244 (*ex* NMV P136150), tangential section; C, NMV P141691 (*ex* MUGD 1604), vertical section; D, NMV P136247 (*ex* NMV P136152), vertical section; B–D, Murrindal Limestone, Rocky Camp Quarry. E, F, *Petridiostroma delicatulum* (Ripper, 1937c), holotype NMV P141715 (*ex* MUGD 1606), × 10, Murrindal Limestone, Rocky Camp Quarry; E, tangential section; F, vertical section.
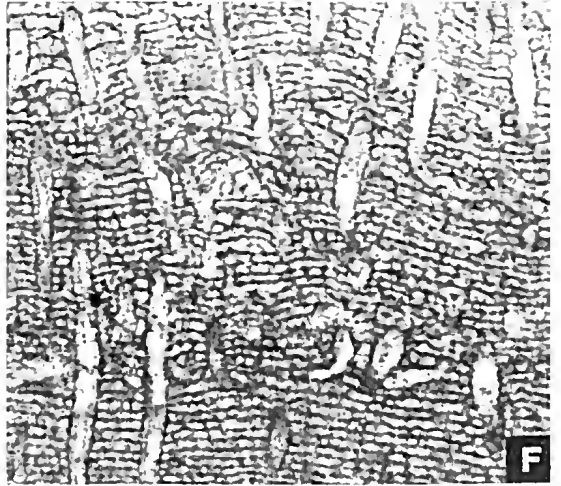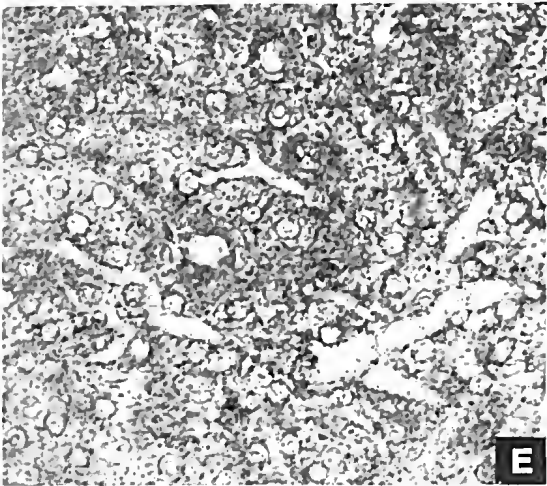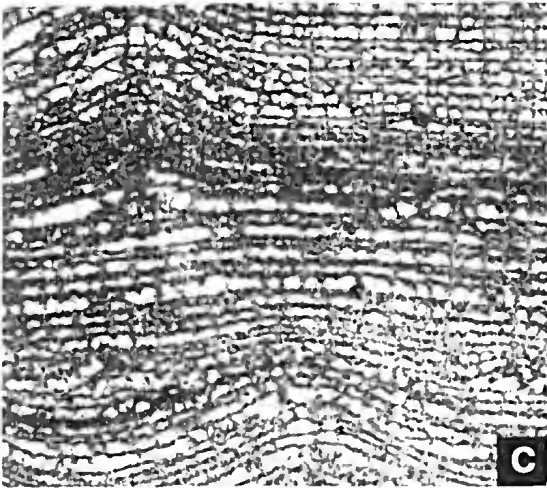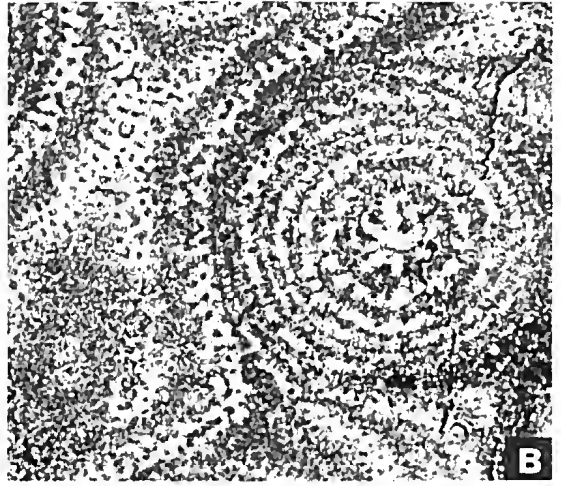
Some of the speeimens (e.g. NMV P141692–93 and P141729) have poorly developed mamelon eolumns, and others (NMV P136249–50, P136251–52, P136253–54, P136255–56, P141700–701, P141708, P141716 and P141750) have mueh of the skeletal elements thickened, presumably by seeondary diagenetie alteration proeesses. Both these groups of speeimens should, however, be regarded as eonspeeifie, and also the finer variety of the speeies referred to by Ripper (1937e: 14) as having more evenly and less flexed laminae. The separation of this variant does not seem justified based on the larger eolleetion of speeimens used in the present study.

The form from Lilydale deseribed previously by Ripper (1933) as *Actinostroma verrucosum* (Goldfuss, 1826) has very similar astrorhizae eentred within mamelon eolumns, as does *G. buchanense*, but differs fundamentally from the latter in exhibiting eollieuli.

Petridiostroma Stearn, 1992

Type species. Simplexodictyon simplex Nestor, 1966.

Remarks. Petridiostroma is a new name for *Petrostroma* Stearn, 1991 (preoeeupied by *Petrostroma* Döderlein, 1892). Speeies assigned to this genus range from the Wenloek to the Famennian.

Petridiostroma clarum (Počta, 1894)

Figs 10A–F, 31A

Clathrodictyon clarum Počta 1894: 152, pl. 18, figs 7–8.—Ripper 1937e: 21, pl. 4, figs 3–4.—Ripper 1938: 236.—Teiehert & Talent 1958: 18, 20.
?*Anostylostroma clarum.*—Coekbain 1965: 747, figs 1–2.
Anostylostroma clarum.—Flügel & Flügel-Kahler 1968: 69 (*cum syn.*).

Material. The material is from the Murrindal Limestone at Rocky Camp Quarry near Buchan, and ineludes previously figured (NMV P141705–06, *ex* MUGD 1605) and other specimens (NMV P136257–58, *ex* NMV P136157; P136259–60, *ex* NMV P136158; P136261–62, *ex* NMV P136159; P136263–64, *ex* NMV P136160; P141723–24). Another doubtfully assigned specimen is from near Hicks's, Murrindal (NMV P141681–82), probably from the Buehan Caves Limestone.

Description. The skeleton has in overall form a gently folded and banded appearanee, the latilaminae being separated by thickened zones of undifferentiated skeletal material, or the skeleton is gently domieal to tabular with no apparent latilamination. Syringoporoid tabulate eorals, 0.3 to 0.4 mm in diameter, are eommonly assoeiated, as well as the symbiotie spiral worm tube *Helicosalpinx* Oekentorp, 1969 in one speeimen (NMV P136261–62). The laminae are mostly laterally extensive but eommonly unevenly spaeed, from 8 to 11 in 2 mm, and from 0.03 to 0.06 (in extremes up to 0.1) mm in thickness; in a few plaees they show breaks in eontinuity, suggestive of pores, and under magnifieation a differentiation of layers, a darker median layer separating lighter-eoloured lower and upper layers; the layers have a transverse fibrosity with minute ?pores less than 0.01 mm aeross.

The pillars are simple, spool-shaped (rarely superimposed), and most eommonly rounded in eross seetion; only a few are Y-shaped; they are normally irregularly spaeed throughout the skeleton; in vertieal seetions the most elosely spaeed are from 6 to 9 in 2 mm; in tangential seetions they have diameters ranging from 0.05 to 0.15 (normally about 0.1) mm aeross; and about 12 oeeupy eaeh 1 mm², in a few plaees, seemingly mainly assoeiated with diseontinuity surfaees, a phase developed in whieh the pillars are irregular to vermiform, or form irregular networks between sueeessive laminae. Small cyst-like dissepiments are eommonly represented in the larger interlaminar spaees, but astrorhizae are absent.

Remarks. Apart from the more eonspieuous banding of skeletal material in some speeimens, the Vietorian material is elosely similar to the type material of *P. clarum* from the Middle Devonian Koněprusy Limestone (f2) of the Prague Basin, Czeeh Republie. The Vietorian speeimens exhibit a wide range of variability in spaeing of laminae and in eontinuity and spaeing of pillars (see Figs 10A–F).

Coekbain (1965) also ineluded speeimens from the Early Devonian (?Emsian) Reefton Limestone of New Zealand in this speeies but they have eonspieuous mamelons, 2–3 mm in

Fig. 10. Petridiostroma clarum (Počta, 1894), × 10, Murrindal Limestone, Rocky Camp Quarry; A, NMV P141705, vertical section; B, NMV P141706, tangential section; C, NMV P136258 (*ex* NMV P136157), tangential section; D, NMV 136257 (*ex* NMV P136157) vertical section; E, NMV P136263 (*ex* NMV P136160), vertical section; F, NMV P136264 (*ex* NMV P136160), tangential section.
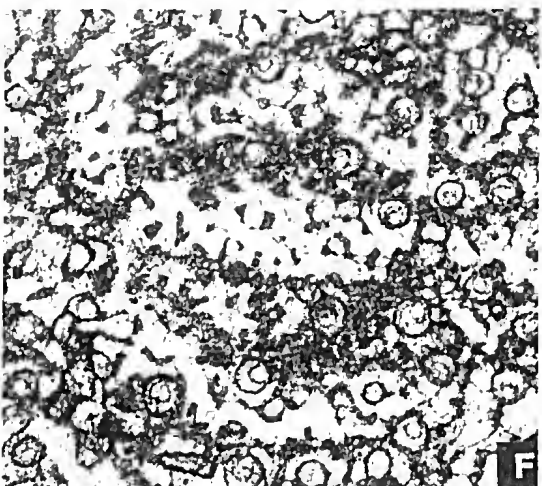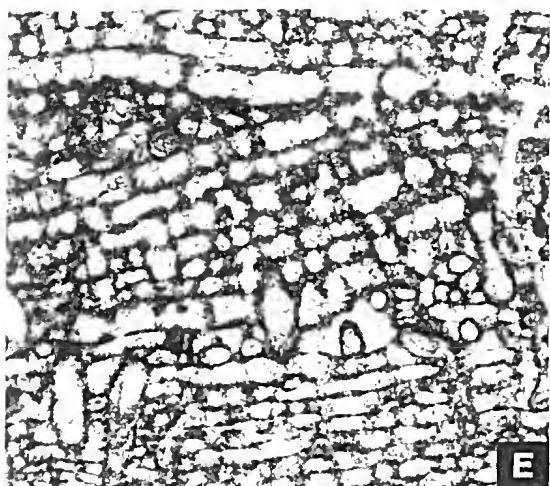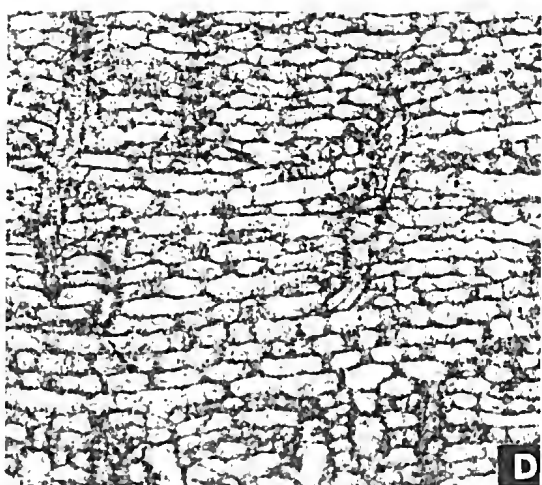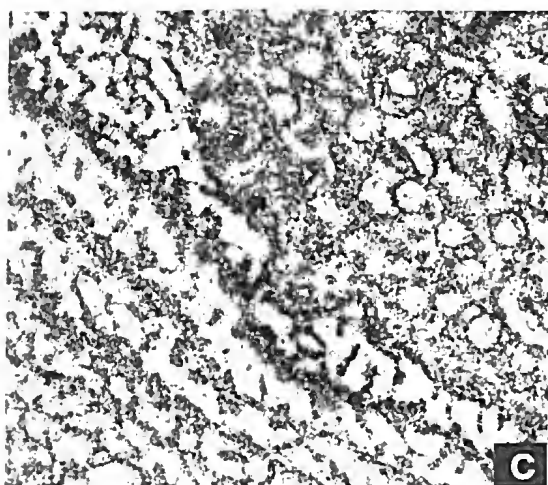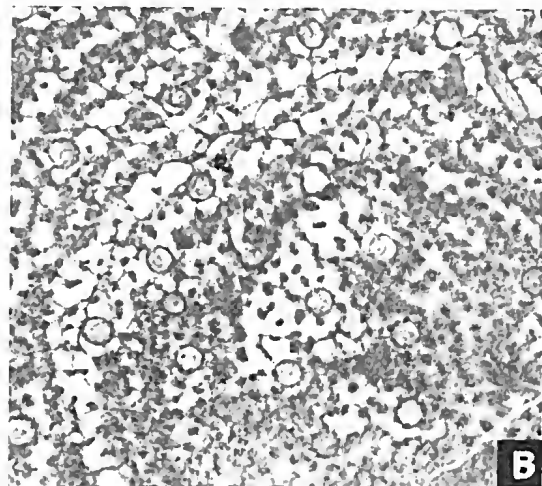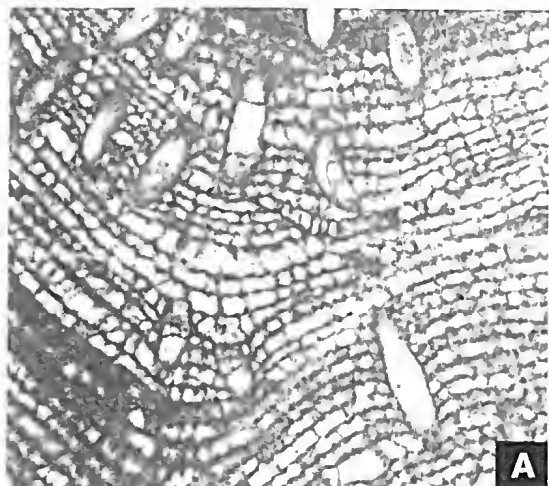
diameter and 5–15 mm apart. Consequently the Reefton specimens are only doubtfully referrable to *P. clarum*, and may be better placed in *Petridiostroma arvense* (Parks, 1936) from the Eifelian Onondaga Formation of Ontario, a species that has well defined mamelons.

Petridiostroma delicatulum (Ripper, 1937c)

Fig. 9E–F

Clathrodictyon convictum var. *delicatula* Ripper 1937c: 20, pl. 4, figs 1–2.—Ripper 1938: 236.— Teichert & Talent 1958: 18, 20.
Clathrodictyon convictum delicatulum.—Flügel & Flügel-Kahler 1968: 103.

Material. Holotype (NMV P141715, *ex* MUGD 1606) from the Murrindal Limestone at Rocky Camp Quarry near Buchan.

Remarks. This fine-textured species is based on one small specimen intergrown with a syringoporoid tabulate coral. Laminae are laterally continous, thin and closely spaced, from 15 to 19 in 2 mm. The interconnected pillars are simple, rounded and rarely superposed, from 0.06–0.09 mm in diameter. A few large canals from 0.25–0.4 mm in diameter, seen in the tangential section, may be astrorhizal structures but these are difficult to differentiate from the connecting tubules of the associated syringoporoid coral.

Petridiostroma sp.

Fig. 11A–B

Clathrodictyon regulare (Rosen, 1867).—Ripper 1937a: 2, pl. 1, figs 1–2.—Ripper 1938: 236 (*partim.*).
non *Clathrodictyon regulare.*—Ripper 1937c: 16, pl. 1, figs. 1–2.
Anostylostroma sp. nov. A.—Philip 1962: 129.

Material. One previously figured specimen (NMV P141827–28, *ex* MUGD 1599), and three other specimens (NMV P141814–15, P141812 and P141818) from the Loyola Limestone at Griffith's Quarry, about 17 km south of Mansfield.

Remarks. The Loyola specimens are poorly preserved and too incomplete to resolve all skeletal features and details of microstructure. Consequently the species is left in open nomenclature. The original assignment of the material to

Clathrodictyon regulare is unjustified given that the type material from the Llandovery of Estonia, revised by Nestor (1964), has a much finer texture, with 18 laminae and 14 pillars spaced in 2 mm, as compared with the spacing in the Loyola specimens of 7–9 laminae and 6–8 pillars in 2 mm. The Loyola species has continuous and relatively evenly spaced laminae (about 0.1 mm thick), in gross form regularly undulose, and simple, rounded, only rarely superposed pillars, also about 0.1 mm in diameter. These Loyola specimens do not show upwardly branching and spreading pillars, and scattered pores penetrating the laminae, as in *Anostylostroma* (see Stearn 1991).

Clathrodictyon Nicholson & Murie, 1879

Type species. C. vesiculosum Nicholson & Murie, 1879.

Clathrodictyon sp.

Fig. 12F

Clathrodictyon confertum Nicholson, 1889.—Ripper 1937c: 18, pl. 3, fig. 3.

Material. One specimen (NMV P141740–41, *ex* MUGD 1607) from the Buchan Caves Limestone, Martin Cameron's Quarry near Buchan. NMV P141741 was previously figured by Ripper (1937c) as pl. 3, fig. 3.

Remarks. This specimen exhibits the highly inflected laminae of a true *Clathrodictyon* but should not be grouped with *Clathrodictyon confertum* from the Middle Devonian of south Devon, England, which has a much more finely textured vesicular mesh of laminae and inflected pillars within regularly spaced, 1 mm thick latilaminae.

Clathrodictyon? heathsense sp. nov.

Figs 11C–F, 12A

non *Clathrodictyon convictum* Yavorsky 1929: 91, 105, pl. 6, fig. 10, pl. 9, figs 5–7.
Clathrodictyon convictum.—Ripper 1937c: 19, pl. 3, figs 4–8.—Ripper 1938: 236.—Teichert & Talent 1958: 16.—Philip 1960: 153.
aff. *Clathrodictyon regulare* (Rosen, 1867).—Ripper 1937c: 16, pl. 3, figs 1–2.

Fig. 11. A, B, *Petridiostroma* sp., × 10, Loyola Limestone, Loyola; A, NMV P141827 (*ex* MUGD 1599), vertical section; B, NMV P141828 (*ex* MUGD 1599), oblique section. C–F, *Clathrodictyon? heathsense* sp. nov., × 10, Buchan Caves Limestone, Heath's Quarry; C, holotype NMV P141799 (*ex* MUGD 1616), vertical section; D, paratype A NMV P141769 (*ex* MUGD 1613), tangential section; E, paratype A NMV P141770 (*ex* MUGD 1613), vertical section; F, holotype NMV P141798 (*ex* MUGD 1616), tangential section.
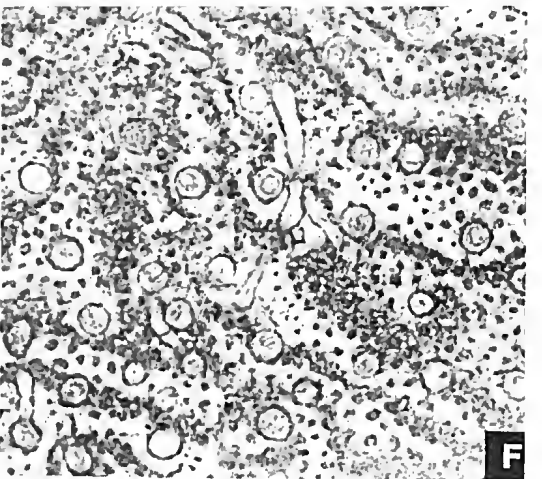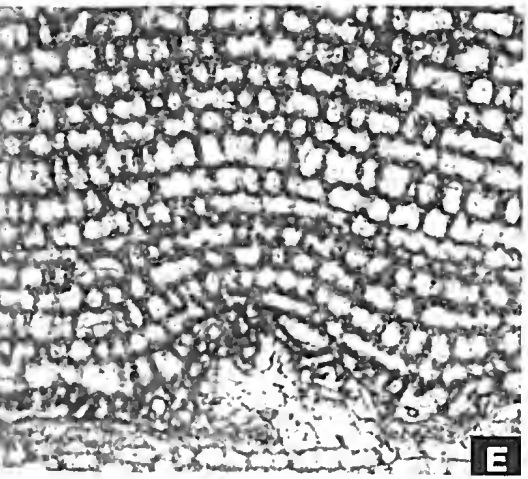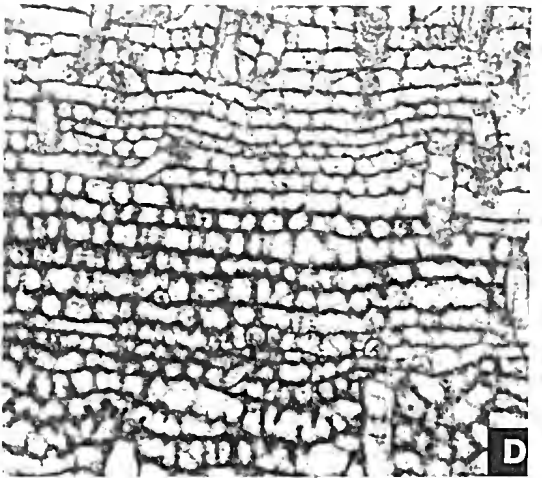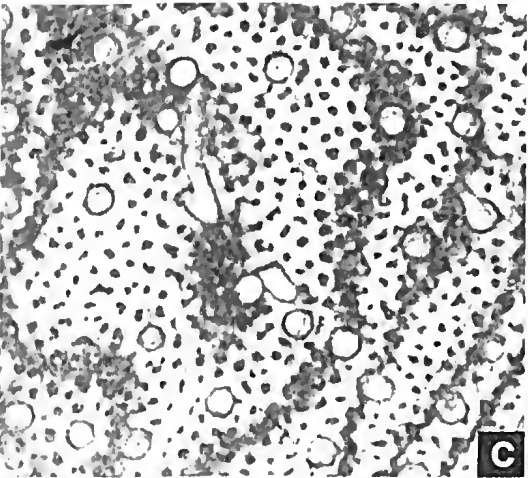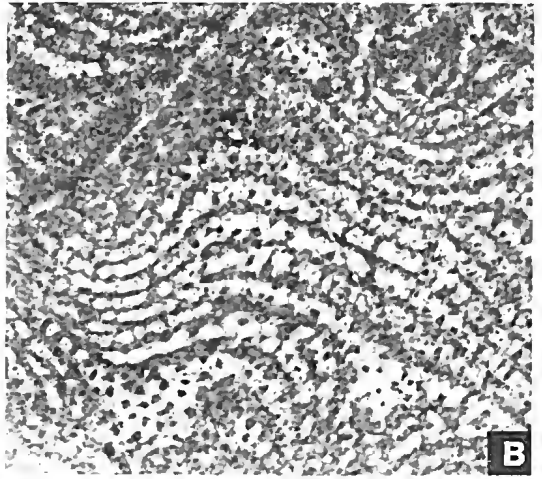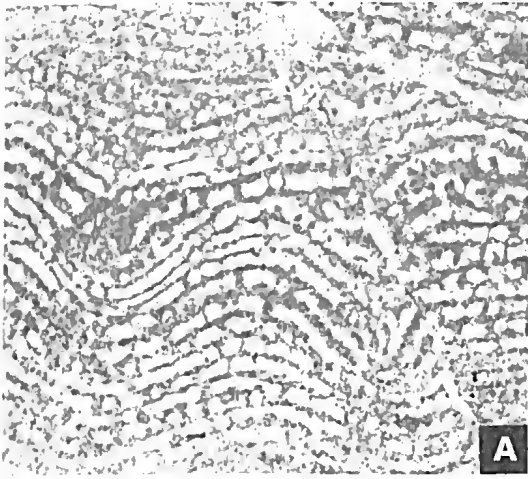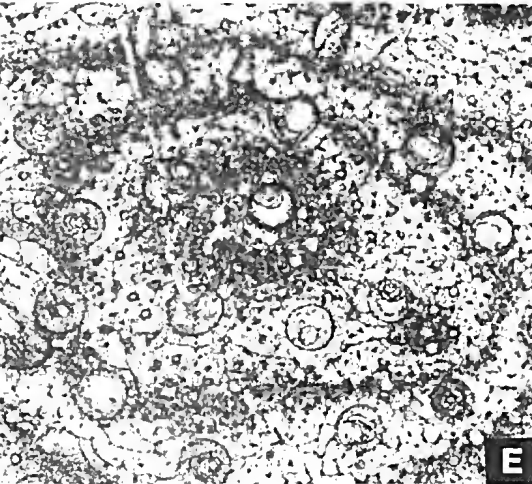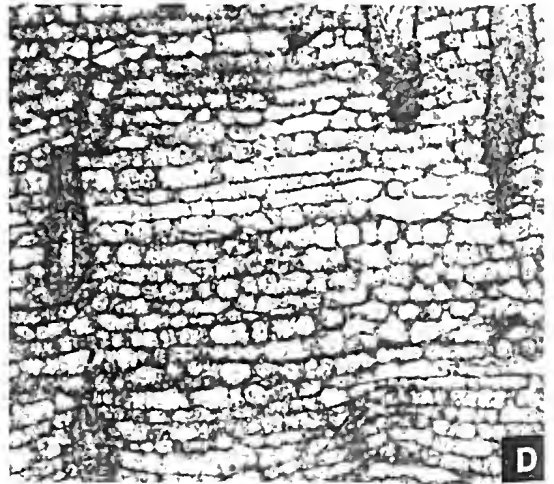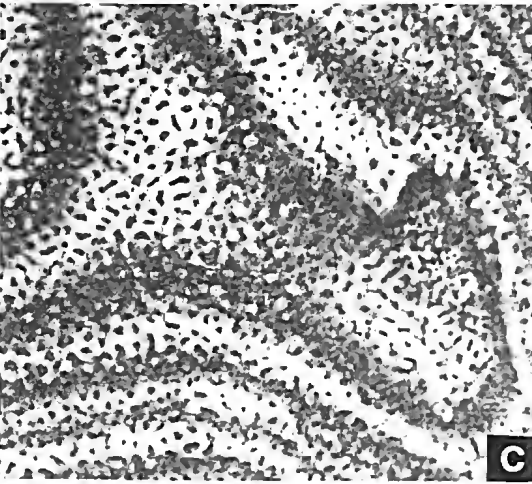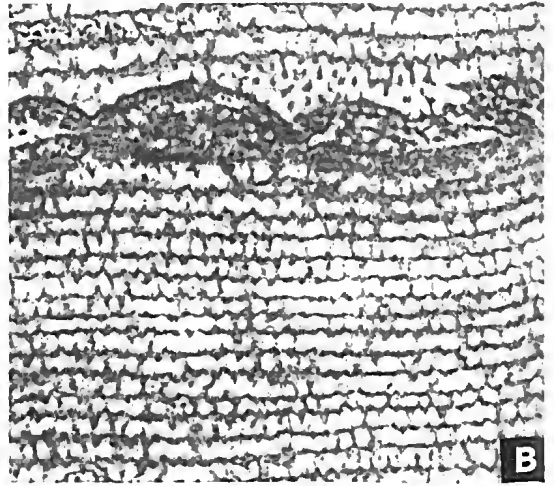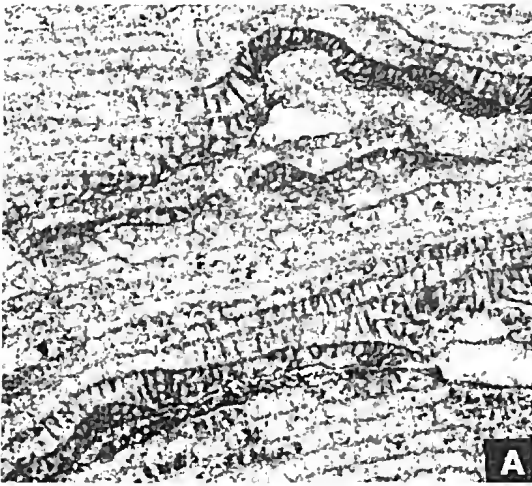
non *Simplexodictyon convictum.*—Nestor 1966: 26, pl. 9, fig. 1; pl. 10, figs 1–2.
non *Petrostroma convictum.*—Stearn 1991: 618.

Material. Holotype (NMV P141798–99, *ex* MUGD 1616), and nine paratypes (NMV P141769–70, *ex* MUGD 1613; NMV P136273–74, *ex* NMV P136163; NMV P136275–76, *ex* NMV P136164; NMV P136277–78, *ex* NMV P136165; NMV P136279–80, *ex* NMV P136166; NMV P136281–82, *ex* NMV P136167; NMV P136283–84, *ex* NMV P136168; NMV P136285–86, *ex* NMV P136169; NMV P136287–88, *ex* NMV P136170) from the Buchan Caves Limestone, Heath's Quarry, near Buchan. Specimens MUGD 1613 and NMV P136164 are designated as paratypes A and B respectively.

Derivation of name. After the locality name, Heath's Quarry.

Diagnosis. This species has laminae inflected upwards and downwards, spaced from 6 to 10 in 2 mm, ring as well as post-like pillars, and a transversely fibrous and minutely porous to compact microstructure.

Description. Specimens are fragments of low domical skeletons estimated to be at least 150 mm in diameter and 90 mm in height. In vertical sections the laminae are broadly continuous, relatively evenly spaced, and gently undulating, in a few skeletons with crests 10 mm or more apart. Laminae may exhibit small-scale crumpling associated with intersecting spool-shaped and ring-pillars, and gentle downflexing at contacts with the associated syringoporoid (caunopore) tabulate coral; individual laminae are from 0.03 to 0.07 (typically 0.05) mm in thickness, and they are spaced from 6 to 10 (most commonly 7–8) in 2 mm. Laminae do not show a tripartite or ordinicellular structure but seem mainly to be transversely fibrous and minutely porous to compact in texture.

Latilaminae not conspicuously developed, but in one paratype (B, NMV P136164) they are from 3 to 6 mm thick; they are defined either by bands of more closely spaced or thickened laminae, or by marked disruptions to growth; a distinctive initial phase forms at the base of a latilamina after such growth interruption, with the development of finer, branching pillar-like

elements similar to those seen in *Schistodictyon.* In the latilaminate specimen NMV P136164 these prominent fine branching elements show on-lapping relationships through successive initial layers as the organism recolonized over the former growth surface (Fig. 12A).

Pillars are rarely superposed throughout the skeleton, and comprise solid, simple, rod-like elements as well as ring pillars formed from inflections of laminae into pillars, both upward and downward; the pillars range from 0.08 to 0.12 mm across and have a spacing from 7 to 9 in 2 mm.

In tangential sections the laminae are represented as more opaque, obliquely intersected concentric bands with scattered rounded pores up to 0.1 mm in diameter. Ring-pillars may be from 0.09 to 0.2 mm in outer dimensions, and the solid pillars, which have rounded to irregular outlines, also range from 0.07 to 0.12 mm across. Astrorhizae are not confirmed, though a possible vertical canal up to 1.3 mm across occurs in one specimen (NMV P136166). The associated syringoporoid (caunopore) tubes and their offshoots are easily distinguished by their thicker walls; they have diameters ranging from 0.2 to 0.5 mm.

Remarks. The Heath's Quarry material was assigned by Ripper (1937e) to *Clathrodictyon convictum* Yavosky, 1929 from the Upper Silurian (Ludlow) of Saaremaa island, Estonia. Revision of this species by Nestor (1966) suggested assignment to *Simplexodictyon.* However, Stearn's (1991, 1992) redefinition of this genus, now characterised by double laminae, and his introduction of *Petridiostroma* for species with 'simple planar laminae and rodlike pillars', now requires that Yavorsky's *convictum* be transferred to *Petridiostroma.*

The Victorian species assigned previously to *convictum* is distinguished from Yavorsky's (1929) *Petridiostroma convictum* in exhibiting ring-pillars and pores through the laminae. However, the rings are formed by the downward bending of laminae into pillars as in *Clathrodictyon,* as well as by the upward inflection of laminae as in *Stromatoporella.* Consequently the

Fig. 12. A, *Clathrodictyon*? *heathsense* sp. nov., paratype B NMV P136275 (*ex* NMV P136164), vertical section, × 7.5, Buchan Caves Limestone, Heath's Quarry. B, C, *Clathrodictyon*? aff. *heathsense* sp. nov., × 10, Buchan Caves Limestone, Heath's Quarry; B, NMV P141808 (*ex* MUGD 1618), vertical section; C, NMV P141809 (*ex* MUGD 1618), tangential section. D, E, *Clathrodictyon*? cf. *heathsense* sp. nov., × 10, Murrindal Limestone, roadside between Buchan and Murrindal; D, NMV P136289 (*ex* NMV P136171), vertical section; E, NMV P136290 (*ex* NMV P136171), tangential section. F, *Clathrodictyon* sp., NMV P141740 (*ex* MUGD 1607), vertical section, × 10, Buchan Caves Limestone, Martin Cameron's Quarry.

species appears to be transitional between the two genera, though, on the basis that it lacks true ring-pillars and the laminae composed of tripartite, ordinicellular skeletal material, it is retained questionably in *Clathrodictyon*.

Two other similar specimens from the Buchan area were referred by Ripper (1937c: 16) to *Clathrodictyon regulare* (Rosen, 1867). In her description of the species she referred to the appearance of the pillars as 'sometimes tubular' and 'as rings' in tangential section, recalling *Clathrodictyon calamosum* Ripper, 1933 (revised herein to *Tubuliporella calamosa*) from the Lilydale Limestone. Clearly this is a reference to ring-pillars and, overall, apart from the lack of an association with the syringoporoid ('caunopore') corals, these specimens are similar to *C.? heathsense*. Both the previously figured specimen (NMV P141808–09, *ex* MUGD 1618) from Heath's Quarry (Fig. 12B–C), and another (NMV P141677–78), probably also from the Buchan Caves Limestone near Hicks's, Murrindal, exhibit rounded to elongate, solid pillars and ring-pillars, as well as pores within laminae. A few rare traces of astrorhizal canals and dissepiments are also seen in some interlaminar spaces, and similar phase changes of finer, branching, pillar-like elements in the basal layers of latilaminae. These features are not typically represented in the type material of *C.? heathsense*; consequently, the specimens are assigned separately as *C.? aff. heathsense*.

An additional, well preserved specimen (NMV P136289–90, *ex* NMV P136171) from the Murrindal Limestone at the roadside (L4) locality between Buchan and Murrindal exhibits alternations of more laterally extensive, evenly and widely spaced laminae and more closely spaced, irregular and less continuous laminae (Fig. 12D–E); some have a long, low cyst-like appearance. The skeleton is intergrown with an alveolitid coral and with a syringoporoid ('caunopore') having individual corallites from 0.4 to 0.6 mm in diameter. The laminae are thin and seemingly composed of compact skeletal material. Dissepiments occupy interlaminar spaces. The pillars are either simple posts or are ring pillars formed from upwardly inflected laminae. This dissepimented form is allied with

but not identical to *C.? heathsense*; hence it is referred to as *C.? cf. heathsense*.

Clathrodictyon? heathsense from the Buchan Caves Limestone exhibits a wide range of variability. Firstly, it exhibits ring pillars and therefore may be viewed as transitional to some of the early stromatoporellids. *Stromatoporella* cf. *granulata* and *Tubuliporella calamosa*, both from the Pragian Lilydale Limestone, are the earliest known representatives of two stromatoporellid genera. However, neither species is in a line of descent to *C.? heathsense*. Secondly, *C.? heathsense* (Buchan Caves Limestone) and *C.? cf. heathsense* (Murrindal Limestone) may show small inflections of laminae upwards and downwards into pillars, like those exhibited in *Petridiostroma clarum* from the Murrindal Limestone at Rocky Camp Quarry (compare Figs. 10D, 11D–E and 12D), and in this respect the forms may be related.

Clathrodictyon abnorme Yang & Dong, 1979 from the upper Emsian Guitang Member of the Beiliu Formation of Guangxi Province, South China, bears the closest similarity to the Victorian species in having similar dimensions and in exhibiting a few ring pillars, but does not show such regularly pronounced upward and downward inflections of laminae into pillars.

Family TIENODICTYIDAE Bogoyavlenskaya, 1965 (amend. Stearn, 1980)

Schistodictyon Lesovaya, in Lesovaya & Zakharova 1970

Type species. *S. posterius* Lesovaya, in Lesovaya & Zakharova 1970.

Schistodictyon? cylindriferum (Ripper, 1933)

Fig. 13A–D

Clathrodictyon regulare cylindriferum Ripper 1933: 157, figs 3, 6A–B.—Ripper 1938: 236.
Anostylostroma cylindrifera.—Philip 1960: 153.

Material. Holotype (four thin sections NMV P141897–98, P141995–96; *ex* NMV P13746) is from the Lilydale Limestone at Mitchell's (Cave Hill) Quarry, Lilydale; another well preserved Lilydale specimen (thin section NMV P141867) is from the collection of F. S. Colliver. Two additional Lilydale specimens (thin sections NMV P142001, *ex* NMV P13789;

Fig. 13. A–D, *Schistodictyon? cylindriferum* (Ripper, 1933), × 10, Lilydale Limestone, Mitchell's (Cave Hill) Quarry; A, holotype NMV P141995 (*ex* NMV P13746), tangential section; B, holotype NMV P141996 (*ex* NMV P13746), vertical section; C, D, NMV P141867, vertical sections. E, F, *Atelodictyon hicksense* sp. nov., holotype, × 10, Murrindal Limestone, Rocky Camp Quarry; E, NMV P136269 (*ex* NMV P136214), vertical section; F, NMV P136270 (*ex* NMV P136214), tangential section.
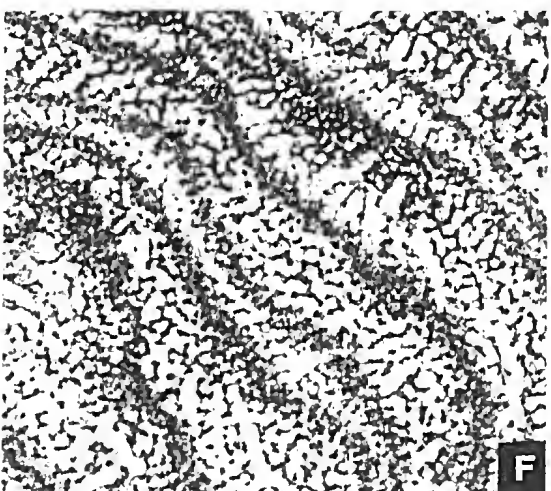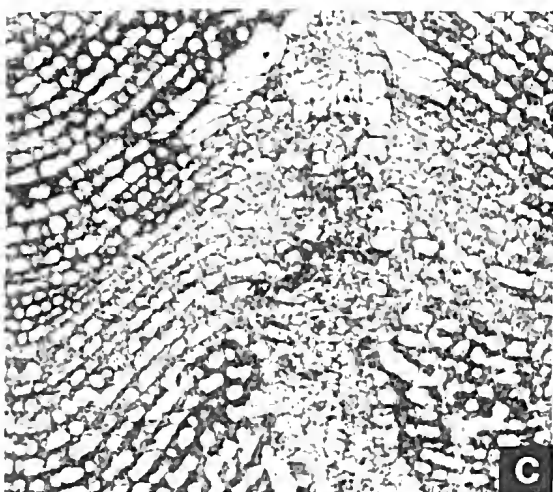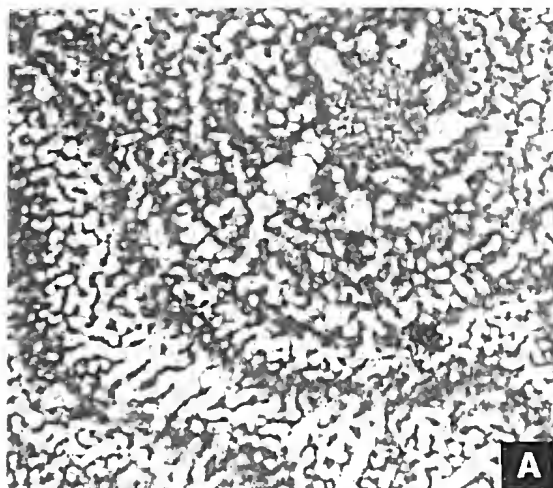
and P141973—74, *ex* NMV P13774) are doubtfully assigned to the species.

Description. In vertical sections the laminae are laterally extensive, regularly spaced and slightly undulating; spaced from 9 to 12 in 2 mm, and typically 0.04 to 0.07 mm thick; apparently composed of compact (minutely speckled) skeletal material. Pillars are simple, rarely superposed, ranging from dumbbell-shaped to more conspicuously widened towards the top, and spaced from 8 to 10 in 2 mm. Dissepiments are rare within gallery spaces. Astrorhizae are conspicuous, with large horizontal canals ranging from 0.2 to 0.5 mm in diameter, with a vertical series of tubes up to 0.5 mm in diameter partitioned by a considerable number of tabulae, and associated with mamelon columns.

In tangential sections the well developed mamelon columns are spaced from 8 to 10 mm apart; the pillars are vermiform to less commonly rounded in cross section; adjacent to laminae (presumably at the tops) they form a network; rounded pillars are from 0.05 to 0.1 mm in diameter and from 0.10 to 0.15 mm apart. A ring-like cluster of seven to eight large vertical astrorhizal canals, about 1.5 mm in diameter, forms around a much finer irregularly reticulated mesh of canals and dissepiments at the centre of each mamelon column.

Remarks. Philip (1960), in reporting this taxon from the Bell Point Limestone at Waratah Bay, also raised the status of Ripper's subspecies to species rank and transferred it to *Anostylostroma*. Stearn (1991) limited the scope of *Anostylostroma,* based on the type species *A. hamiltonense* Parks, 1936, to Middle–Upper Devonian forms with non-superposed, irregularly and complexly upwardly branching pillars and simple planar laminae with scattered pores and a fibrous microstructure. Consequently *cylindriferum* is now excluded from that genus because it has compact, non-porous laminae and less complexly and irregularly upwardly branching pillars.

In cross section the pillars are commonly vermiform, though towards their bases they are rounded and near their tops they exhibit a regular network of ring-pillars. The pillars are not as regularly branched or distinctively V- or Y-shaped as in the type species of *Schistodictyon.* Nevertheless, the pillars are markedly more upwardly spreading and vermiform in cross section than in typical species of *Petridiostroma.* Consequently the species is viewed as having closer relationships with *Schistodictyon* than with *Petridiostroma*, and is therefore assigned to the former with qualification.

Stearn (1991) regarded *Coenostellodictyon* Yavorsky, in Khalfina & Yavorsky 1971, based on *Clathrodictyon krekovi* Yavorsky, 1955 from the Lochkovian of the Kuznets Basin, as a junior synonym of *Schistodictyon*, mainly on the basis of its upwardly branching pillars with cylindical bases. However, it does not exhibit the complexly branching pillars of the type species of *Schistodictyon*, and in this respect more closely resembles the Victorian species.

A species of *Schistodictyon* with inconspicuous astrorhizae and lacking mamelons has been recorded previously from the Lower Devonian Jesse Limestone of central New South Wales (Webby & Zhen 1993).

Pseudoactinodictyon Flügel, 1958c

Type species. P. juxi Flügel, 1958c.

Pseudoactinodictyon sp.

Fig. 15A–F

Material. One specimen (NMV P136265–68, *ex* NMV P136161) from the Coopers Creek Limestone at Tyers Quarry.

Description. This coarse-textured species has gently undulose, mainly laterally continuous, single-layered and compact laminae, as well as abundant dissepiments in most interlaminar spaces. The laminae are from 0.06 to 0.1 mm thick and have a spacing of 3.5 to 5 in 2 mm. Large vesicular dissepiments cross a number of interlaminar spaces in a few places where the laminae are not continuous. Pillars vary from short and confined to interlaminar spaces, to long and randomly distributed through the skeleton; these latter may extend through six or more interlaminar spaces (that is, up to 5 mm

Fig. 14. A, B, *Atelodictyon* sp., × 10, Buchan Caves Limestone, Bindi; A, NMV P141940, vertical section; B, NMV P141939, tangential section. C, D, *Atelodictyon chapmani* (Ripper, 1933), holotype, × 10, Lilydale Limestone, Mitchell's (Cave Hill) Quarry; C, NMV P141900 (*ex* NMV P13747), tangential section; D, NMV P141971 (*ex* NMV P13747), vertical section. E, F, *Stromatoporella* cf. *granulata* (Nicholson, 1873), × 10, Lilydale Limestone, Mitchells's (Cave Hill) Quarry; E, NMV P141853 (*ex* MUGD 1622), vertical section; F, NMV P141852 (*ex* MUGD 1622), tangential section.
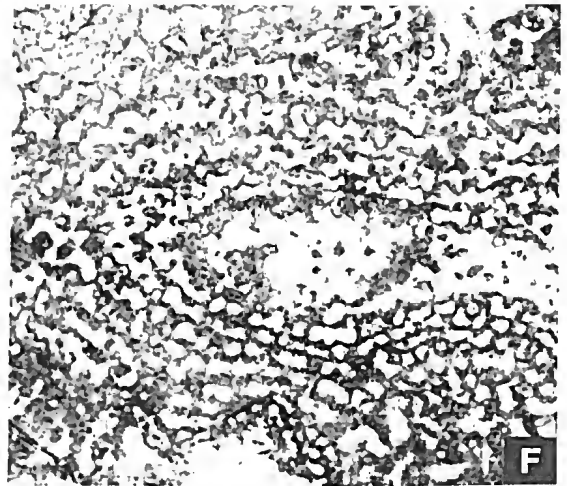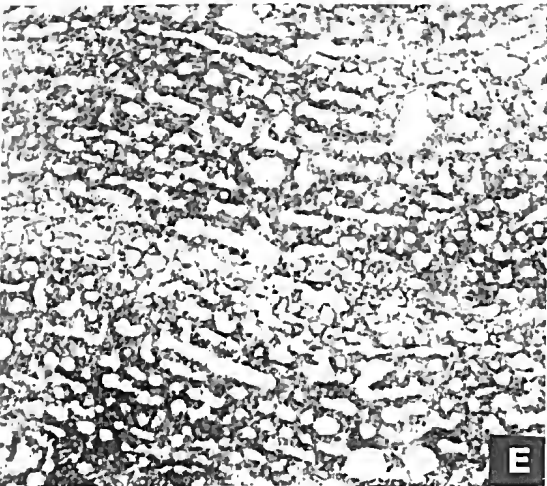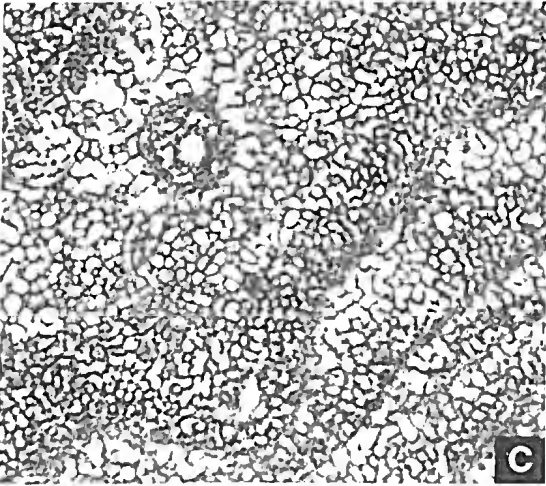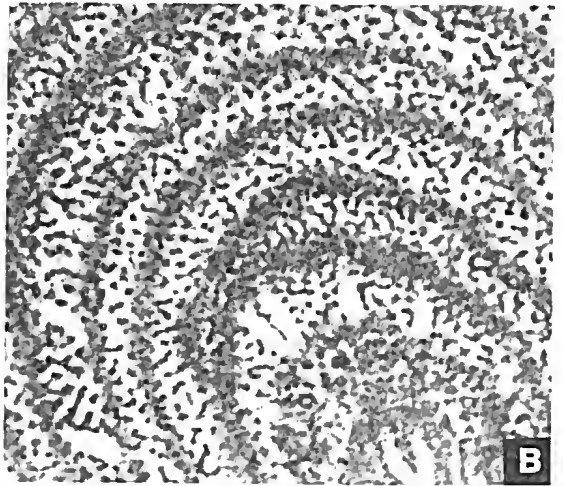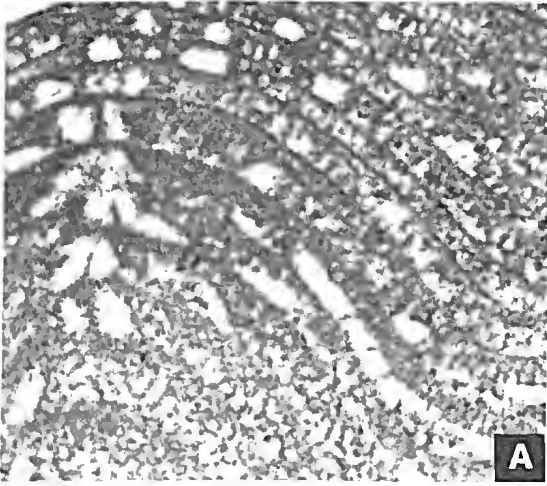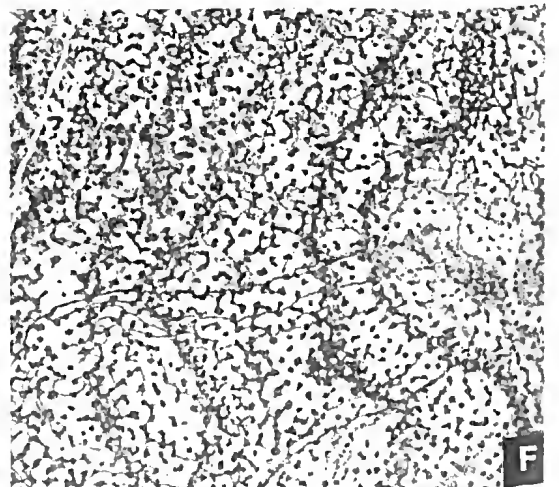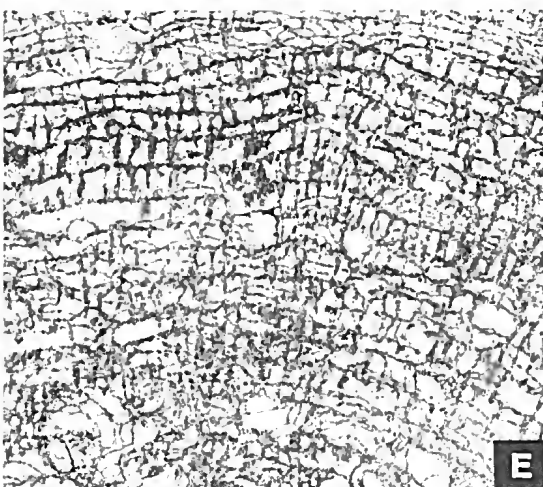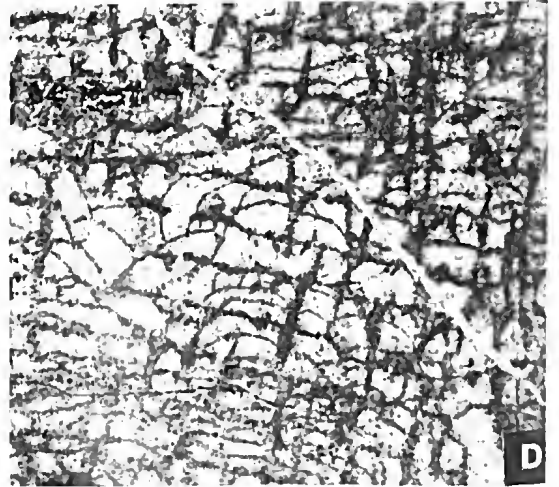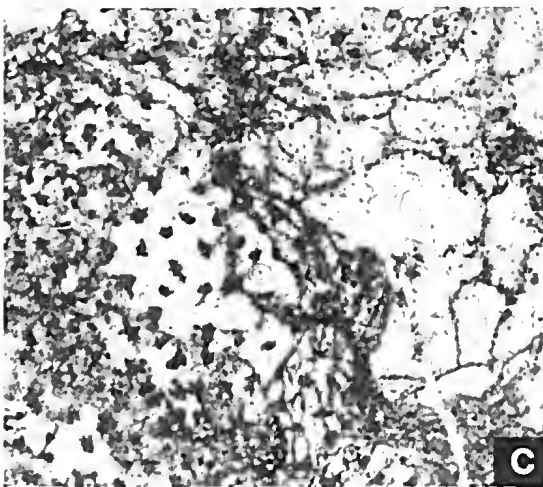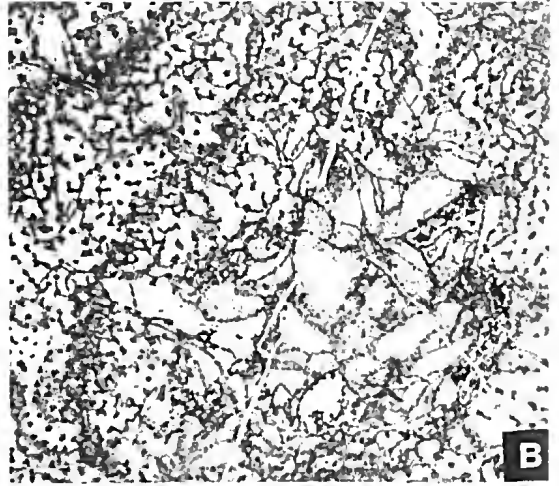
vertically); typically they are from 0.1 to 0.15 mm in diameter and in a few places they also branch. Large astrorhizal canals up to 1 mm in diameter are scattered irregularly within the skeleton; they comprise radiating canals within the galleries joined to a series of superposed vertical passageways.

In tangential sections pillars are mainly rounded to irregular, from 0.1 to 0.25 mm in diameter and from 7 to 10 in 1 mm^2, but they form somewhat irregular and incomplete networks beneath each laminae. The laminae are intersected as darker concentric bands with a few pores, 0.2 mm across. Some dissepiments are large, continuous across at least 4 interlaminar spaces. Astrorhizae comprise very large, complex, tabulate, vertical canals approximately 5 by 3.5 mm across and centred on very broad, low mamelon columns; and radiating canals within galleries from 0.7 to 1 mm wide, crossed by astrorhizal tabulae.

Remarks. This species is left in open nomenclature because it is represented by only one specimen. However, it has long pillars and large dissepiments which in places cross several interlaminar spaces, unlike any of the previously described Middle Devonian species (Fagerstrom 1982, Stearn 1991) and the species currently under description from the Lomandra Limestone (Emsian–Eifelian) of the Broken River Embayment, north Queensland.

Atelodictyon Lecompte, 1951

Type species. A. fallax Lecompte, 1951.

Remarks. Stearn (1991) restricted the scope of *Atelodictyon* to forms with simple, planar laminae like the type species. He excluded those with laminae composed of colliculi, these latter being included in *Aculatostroma* Khalfina, 1968b.

Atelodictyon chapmani (Ripper, 1933)

Fig. 14C–D

Clathrodictyon chapmani Ripper 1933: 159, figs 4, 6C–D.—Ripper 1938: 236.
?*Clathrodictyon* aff. *chapmani*.—Ripper 1937a: 3, figs 3–4.
Atelodictyon chapmani.—Lecompte 1951: 134.— Stearn 1966: 88.

?*Atelodictyon* (or ?*Tienodictyon*) *chapmani*.—Flügel & Flügel-Kahler 1968: 67.

Material. Holotype (NMV P141899–900, P141971–72; *ex* NMV P13747) from the Lilydale Limestone, Mitchell's (Cave Hill) Quarry, Lilydale. Three other Lilydale specimens are closely allied, namely NMV P141968–69 (*ex* NMV P13770), P37641 and P141848–49 (these latter previously referred to *Actinostroma* aff. *stellulatum*). Specimens from the possibly correlative Loyola Limestone at Griffith's Quarry near Mansfield are doubtfully referred to the species; these include Ripper's (1937a) figured specimen (NMV P141820–21, *ex* MUGD 1598) and two other specimens (NMV P141813 and P141840–43).

Description. The skeleton is domical with non-enveloping margins. Latilaminae are obscure. Astrorhizae are well developed and mainly appear to be locally associated with mamelon columns of limited relief. In vertical sections laminae are represented by laterally continuous, gently flexed and apparently single, dark, compact layers about 0.05 mm thick, but in some places they are not easily differentiated from underlying interlaminar space with secondarily thickened skeletal elements (apparently mainly coenosteles); spacing of laminae from 4 to 5 in 2 mm. A few dissepiments, and less laterally continuous secondary laminae (or microlaminae) of variable size and of irregular distribution, occur within the interlaminar spaces and link some of the vertical skeletal elements (coenosteles) in an irregular network. Coenosteles typically completely cross interlaminar spaces but in a few places may fall short of the lower parts of the spaces; not clearly superposed; and may be irregular but rarely branching; spaced from 12 to 14 in 2 mm. Astrorhizae are centred mainly on the gently upwardly domed mamelon columns, with the largest vertical tubes being up to 0.6 mm in diameter. Radiating canals present in the adjacent interlaminar spaces, from 0.2 to 0.3 mm in diameter, and crossed by dissepiments.

In tangential sections the coenosteles form an almost continuous, regular, chain-like meshwork between the laminae, that is more complete in the upper two-thirds and typically more closely spaced in the uppermost one-third of each interlaminar space. They have a wall thickness of 0.03–0.04 mm and under magnification appear as a row of small, closely-spaced,

Fig. 15. Pseudactinodictyon sp., Coopers Creek Limestone, Tyers Quarry; A, E, NMV P136268 (*ex* NMV P136161), vertical sections; B, F, NMV P136266 (*ex* NMV P136161), tangential sections; C, NMV P136267 (*ex* NMV P136161), tangential section; A, B, E, F, × 5; C, D, × 10.

rounded dots (seemingly rounded pillars in contact) rather than as a continuous wall. The distance across individual meshes ranges from 0.2 in the lower part of the interlaminar space to 0.1 mm in the upper part.

Remarks. This species was recognized previously by Lecompte (1951: 134) and Stearn (1966: 88) as belonging to *Atelodictyon*. Flügel & Flügel-Kahler (1968: 67), on the other hand, allied it doubtfully with both *Atelodictyon* and *Tienodictyon*.

The specimens from the Loyola Limestone (Ripper 1937a) may be conspecific but are much less well preserved and consequently difficult to assess. The material shows a similar meshwork of coenosteles and abundant astrorhizae in tangential section (illustrated in part by Ripper 1937a, fig. 4) but the laminae are thicker and much more closely spaced (from 8 to 10 in 2 mm). A few breaks occur in the laminae in vertical section but, given the uniformly poor preservation of the material, these may not have real significance.

Another possible species of *Atelodictyon* is recorded from Bindi (Fig. 14A–B). It was previously identified in the Museum of Victoria collections as *Clathrodictyon bohemicum* Počta, 1894 and includes NMV P141938–40, P37639–40 (*ex* NMV P13795). It differs from *A. chapmani* mainly in lacking the closely spaced meshwork of coenosteles, and in places it exhibits rounded pillars.

Atelodictyon hicksense sp. nov.

Fig. 13E–F

Material. Holotype (NMV P136269–70, *ex* NMV P136214) from the Murrindal Limestone, Rocky Camp Quarry near Buchan. One other specimen is designated, namely NMV P141670 from the Ripper collection, from near Hicks's, Murrindal, possibly from the Buchan Caves Limestone.

Derivation of name. From the locality Hicks's near Murrindal, in the Buchan area.

Diagnosis. Species of *Atelodictyon* with closely spaced, complete laminae as well as a few incomplete, long, low, cyst-like laminae, and incomplete to partially complete networks of vertical elements (pillars and coenosteles) except at tops of interlaminar spaces.

Description. Skeleton has laminar external growth form; holotype represented by fragmentary specimen, 150 mm across and 30 mm in height. At most levels within the skeleton the laminae are even and moderately closely spaced, from 8 to 10 in 2 mm, but in a few areas they are very closely spaced; some are not laterally continuous, having the appearance of long, low, cyst-like elements; thickness of laminae varies from 0.03 to 0.05 mm. Vertical elements (pillars and coenosteles) are commonly complete and in some places superposed through more than one interlaminar space. Locally, vertical elements are incomplete, for example at their bases, or they have branching offsets (which typically appear in vertical section as rounded dots towards the middle of interlaminar spaces). Pillars and coenosteles are spaced from 11 to 13 in 2 mm. Astrorhizae are commonly developed throughout the skeleton and are composed of randomly scattered, large, spar-filled spaces, 0.25–0.3 mm in diameter within interlaminar spaces clear of vertical elements, as well as tabulated vertical canals up to 0.4 mm wide.

Laminae are represented by dense concentric bands of skeletal material, in tangential section each layer exhibiting a fine meshwork of dark brown, closely spaced dots surrounded by solid, lighter brown skeletal material. Vertical elements cut in tangential section as pillars and coenosteles. Pillars cut as dots 0.05 to 0.08 mm in diameter interspersed with vermiform pillars and coenosteles forming incomplete networks with meshes about 0.2 mm across in the lower and middle parts of interlaminar spaces and 0.1 mm across at the top.

Remarks. This species comes from higher stratigraphic levels than *A. chapmani*. It occurs in association with *Gerronostroma buchanense* near Hicks's, Murrindal. It differs from *A. chapmani* in having thinner, more closely spaced laminae, even a few incomplete, long, low, cyst-like laminae, and it has a less completely fused network of vertical elements (pillars and coenosteles), except at the tops of interlaminar spaces.

Of the species of *Atelodictyon* listed by Stearn (1991), the type species, *Atelodictyon fallax* Lecompte, 1951 from the Middle Devonian of Belgium, is similar to *A. hicksense* but has relatively widely spaced laminae (5 to 8 in 2 mm), lacks the incomplete, long, low, cyst-like laminae, and displays more continuity of the vertical structural elements within the skeleton. *A. durum* (Khromych, 1974) from the Middle Devonian of the Omulevski Mountains, Siberia, also resembles *A. hicksense* except that it has thicker vertical elements, from 0.1 to 0.13 mm

in diameter, and lacks closely spaced, incomplete laminae.

Order STROMATOPORELLIDA Stearn, 1980
Family STROMATOPORELLIDAE Lecompte, 1951

Genus Stromatoporella Nicholson, 1886b

Type species. Stromatopora granulata Nicholson, 1873.

Stromatoporella cf. granulata (Nicholson, 1873)

Fig. 14E–F

cf. *Stromatopora granulata* Nicholson 1873: 94, pl. 4, figs 3, 3a.
cf. *Stromatoporella granulata.*—Nicholson 1891: 202, pl. 1, figs 4, 5, 14, 15, pl. 4, fig. 6, pl. 7, figs 5, 6, pl. 26, fig. 1.—Flügel & Flügel-Kahler 1968: 180 (*cum. syn.*).—Sleumer 1969: 38, pl. 24, figs 3, 4, pls 25, 26, pl. 27, figs 1, 2.—Zukalová 1971: 52, pl. 11, figs 1–4.—Fagerstrom 1982: 38, pl. 7, fig.1.—Mistiaen 1985: 122, pl. 9, figs 1–9 (*cum syn.*).
Stromatoporella granulata.—Ripper 1937b: 191, pl. 9, figs 3–5.—Philip 1962: 129, 130.
Stromatoporella cf. *damnionensis* (*sic*).—Ripper 1937a: 192, pl. 9, figs 7–8.
non *Stromatoporella granulata.*—Mallett 1970a: 36, pl. 1, figs 1-2.

Material. Two specimens (NMV P141852–53, *ex* MUGD 1622; and NMV P141929, P141999–2000, *ex* NMV P13788) from the Lilydale Limestone, Cave Hill Quarry, Lilydale. Another specimen (NMV P136271–72, *ex* NMV P136162) from the Loyola Limestone at Lime Kiln Quarry, south of Mansfield, is doubtfully included in the taxon.

Description. This species has a skeleton of variably thickened and variably spaced laminae intersected by short, spool-shaped and upwardly flexed ring-pillars. Latilaminae are defined by periodic growth interruptions, commonly at intervals of about 3 mm, and adjacent phase changes to more irregular and finer meshes. Overall the laminae have a gently to more sharply flexed form, giving rise to mamelon-like columns from about 3 to 13 mm apart. Laminae are from 0.08 to 0.13 mm thick and spaced from 8 to 11 in 2 mm. The preservation of laminae and other elements is rather poor, mainly apparently compact but with small areas of speckled (?fine cellular) skeletal material; no axial clear zone or ordinicellular microstructure was seen. Astrorhizae are composed of a somewhat irregular and randomly distributed system of horizontal canals, from 0.2 to 0.5 mm across, extending upwards into larger vertical canals up to 1.2 mm

in diameter in association with mamelon columns. Ring-pillars are conspicuous in tangential section, both within interlaminar spaces and along the margins of obliquely intersected laminae, from 0.08 to 0.13 mm in inside diameter and from 0.15 to 0.25 mm in outside diameter. A few pillars are also short, solid, spool-shaped posts, from 0.08 to 0.12 mm in diameter.

Remarks. In comparison with *Stromatoporella granulata*, the Lilydale specimens have slightly finer overall texture, mamelon-like columns and, perhaps owing to the preservation of the material, lack the tripartite, ordinicellular skeletal material. The specimens are consequently assigned with qualification to this species which, notably, occurs in later, Middle Devonian (mainly Givetian) successions in North America and Europe. Ripper (1937c) originally regarded the two Lilydale specimens as belonging to separate species, on the basis that the specimen assigned to *granulata* had indubitable ring-pillars but the other did not. However, though poorly preserved, this second specimen (originally compared by Ripper to *S. damnoniensis*) also exhibits evidence of ring-pillars in tangential section (see thin section NMV P142000).

Philip (1960: 153) referred to the Lilydale occurrence of *S.* cf. *granulata* as a new variety but this has not since been formalized. He also noted its presence in the Bell Point Limestone at Waratah Bay and in the Coopers Creek Formation of the Tyers area (Philip 1962). The taxon possibly also occurs in the Loyola Limestone near Mansfield (Fig. 16A, B) but, owing to its poor preservation, this specimen is only doubtfully included in the species.

Mallett (1970a) assigned specimens from the Dip Creek Limestone Member (Eifelian) of the Broken River Formation, north Queensland, to *Stromatoporella granulata* but this determination must now be questioned. *S. granulata*, on the basis of Nicholson's original type specimen (no. 329 in the Natural History Museum, London), has a coarser texture than the north Queensland form, with thicker laminae and larger ring pillars.

Genus Stictostroma Parks, 1936

Type species. Stromatopora mammillata Nicholson, 1873, non Schmidt, 1858, = *Stictostroma mammiliferum* Galloway & St Jean, 1957.

Stictostroma sp.

Figs 16C–E, 31B

Material. One specimen (NMV P136291–92, *ex* NMV P136172) from Rocky Camp Quarry near Buchan, and two other specimens (NMV P136293–94, *ex* NMV P136173; and NMV P136295–96, *ex* NMV P136174) from locality L4 south of Murrindal School; Murrindal Limestone.

Description. The well preserved specimen from Rocky Camp shows a remarkable range of internal morphologies throughout its 19 mm of vertical latilaminar growth. It changes from disturbed and irregular basal layers to more regular, widely and closely spaced phases within its 3 to 5 mm thick latilaminae. The skeleton has a weakly mammillate form and a few associated caunopore tubes up to 0.5 mm wide. A few dome-like masses of disordered skeletal material up to 3 mm across and from 1.5 to 2 mm high occur at basal discontinuity surfaces, possibly representing material which formed around localized foreign bodies after pauses in growth.

The widely spaced regular units of skeletal material are composed of continuous, relatively evenly spaced, tripartite laminae, and well developed, post-like to upwardly expanding pillars, commonly confined to interlaminar spaces but in a few places superposed through up to four interlaminar spaces; in other places incomplete, limited to the middle to upper parts of interlaminar space. Pillars are commonly from 0.1 to 0.12 mm across and spaced up to 9 in 2 mm. The laminae show a relatively light axial zone between thicker layers above and below, and overprinted by a transversely fibrous and porous microstructure. Laminae are about 0.1 (in some places to 0.2) mm thick and spaced from 6 to 8 in 2 mm. Dissepiments are abundant.

The more closely spaced phases have laminae which are single-layered (not tripartite), from 0.03 to 0.05 mm thick and spaced from 10 to 13 in 2 mm. The pillars are from 0.08 to 0.1 mm thick.

In tangential section the laminae appear as dark concentric bands with rare pores, about 0.1 mm across. The rounded to irregular pillars are clearly demarcated from the laminae, from 0.1 to 0.2 (commonly 0.15) mm in diameter, and

about 12 to 15 in 1 mm²; but locally, presumably in closer-spaced phases, the pillars are more slender, from 0.08 to 0.12 mm. Larger interlaminar spaces have many dissepiments.

Both specimens from locality L4 (e.g. Fig. 16E) have associated caunopore tubes and, though they do not show the same closely spaced latilaminae and a similar range of variability, they exhibit the same regular, tripartite laminae, spaced from 6 to 8 in 2 mm, and similarly short, post-like to upwardly flaring pillars (only rarely superposed) with dissepiments commonly occupying interlaminar spaces.

Remarks. The species is confidently assigned to *Stictostroma* despite the superposition of a few of its pillars. The species figured by Galloway & St Jean (1957, pl. 6, fig. 4) as *Stictostroma mamilliferum*, which comes from the Middle Devonian Onondaga Limestone of Ontario, is similarly shown with a few of its pillars superposed through up to four interlaminar spaces.

Genus Tubuliporella Khalfina, 1968a

Type species. T. lecompti (*sic*) Khalfina, 1968a. Species name should be spelled *lecomptei* (*nom. correct.*).

Diagnosis. Skeleton is composed of continous laminae and superposed ring-pillars forming tubes, in places divided by tabulae and by thin, post-like pillars confined to interlaminar spaces; laminae may be upwardly(?) inflected into ring-pillars; and skeletal material is porous (amended, after Khalfina 1968a: 150).

Remarks. Khalfina (1968a) also referred to superposed astrorhizae as a diagnostic feature of *Tubuliporella*, but species she assigned to the genus, including *Stromatoporella columbusensis* Galloway & St Jean, 1957, lack astrorhizae.

Tubuliporella was distinguished from *Stromatoporella* by Khalfina (1968a) and Stearn (1980) on the basis of its long, superimposed, tube-like pillars. Three species were first recorded by Khalfina: the type, *T. lecomptei,* from the Middle Devonian (Eifelian) of Salair, and *T. altaica* and *T. tubulipilata* from the Lower Devonian of the Altai Mountains, south-west

Fig. 16. A–B, *Stromatoporella* cf. *granulata*? (Nicholson, 1873), × 10, Loyola Limestone, Lime Kiln Quarry; A, NMV P136271 (*ex* NMV P136162), tangential section; B, NMV P136272 (*ex* NMV P136162), vertical section. C–E, *Stictostroma* sp., × 10; C, NMV P136291 (*ex* NMV P136172), vertical section; D, NMV P136292 (*ex* NMV P136172), tangential section; C, D, Murrindal Limestone, Rocky Camp Quarry; E, NMV P136296 (*ex* NMV P136174), tangential section, Murrindal Limestone, roadside between Buchan and Murrindal. F, *Tubuliporella calamosa* (Ripper, 1933), paratype B NMV P141892 (*ex* MUGD 1448), vertical section, × 10, Mitchell's (Cave Hill) Quarry, Lilydale Limestone.
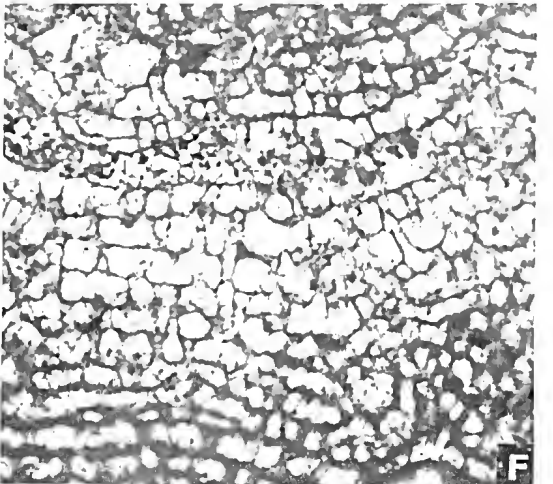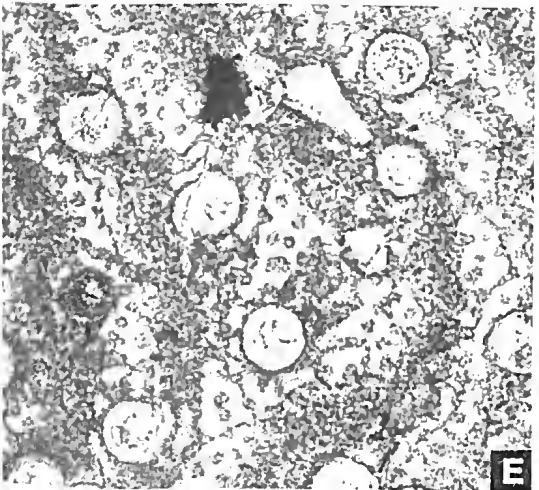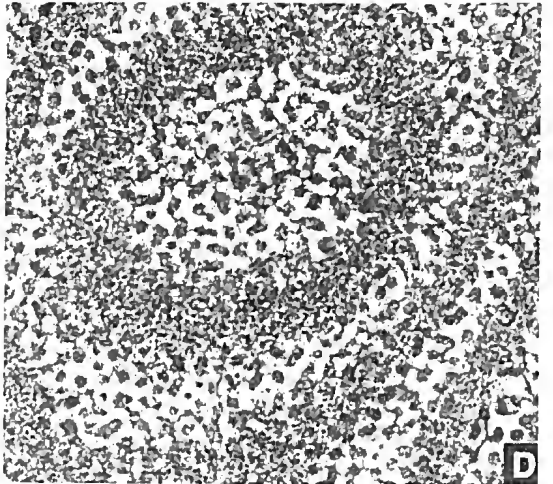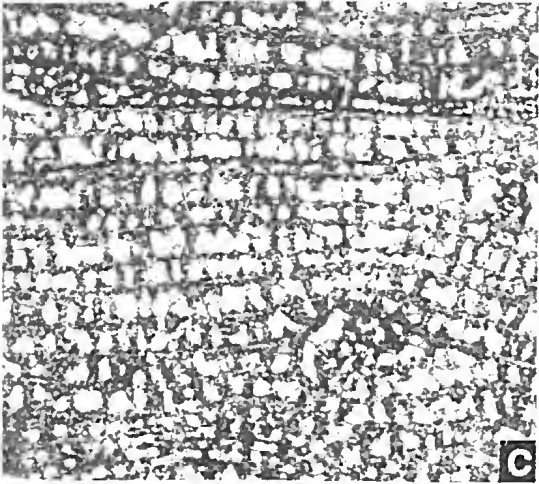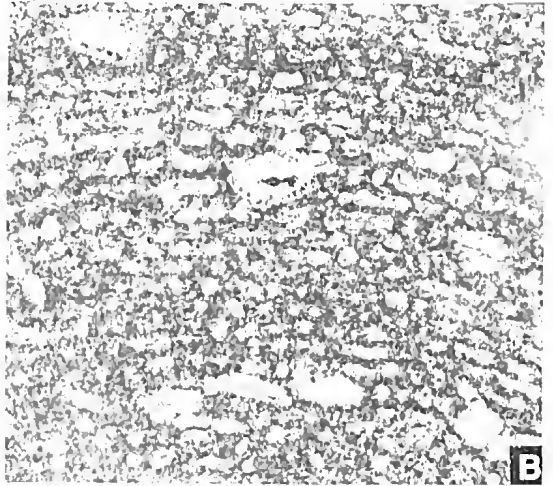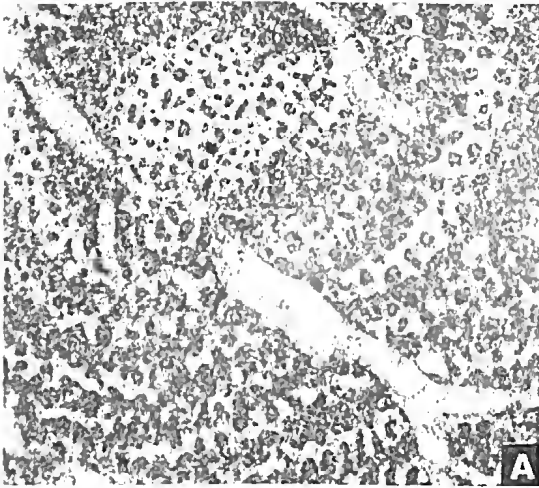
Siberia. Two additional species (*T. kurjenskien-sis* and *T. tubula*) were described by Ivaniya & Kosareva (1968) from the Middle Devonian of the Altai Mountains.

Tubuliporella calamosa (Ripper, 1933)

Figs 16F, 17A–D

Clathrodictyon calamosum Ripper 1933: 160, figs 6E–F.—Ripper 1938: 236.
Clathrodictyon? calamosum.—Flügel & Flügel-Kahler 1968: 56.

Material. Holotype (NMV P141965–67, *ex* NMV P13748), paratype A (NMV P141901–02, P141984–85; *ex* NMV P13749) and paratype B (NMV P141891–92, *ex* MUGD 1448), all from the Lilydale Limestone, Mitchell's (Cave Hill) Quarry at Lilydale. One additional Lilydale form (NMV P141893) also belongs to the species.

Description. In vertical section the laminae are commonly continous, gently undulating and in a few places deflected upwards into superposed, tube-like pillars; spaced from 6 to 9 in 2 mm; typically composed of compact skeletal material though in places becoming transversely fibrous. Laminae of variable thickness, from 0.03 to 0.1 mm (mainly from 0.05 to 0.07 mm). At the ragged outer margin of the skeleton sediment tongues from 5 to 7 mm apart project inward at the latilaminae boundaries. A few upwardly convex dissepiments occur within interlaminar spaces; typically they have thin walls from 0.02 to 0.03 mm thick. Astrorhizae not confirmed. Pillars are formed by superposition of upturned laminae (ring-pillars) extending through 3 or 4 interlaminar spaces, with tube diameters from 0.15 to 0.2 mm across and rare tabulae, and as simple post-like pillars slightly expanded at the laminae. Commonly galleries are rounded to subrectangular, ranging from 0.2 mm wide and 0.15 mm high to 0.5 mm wide and 0.3 mm high.

The tangential section shows abundant tube-like pillars developed throughout the skeleton, from 0.13 to 0.23 mm (usually 0.15–0.20) mm in diameter; these are typically spaced from 0.2 to 0.4 mm apart. Some randomly scattered solid, post-like, pillars are cut as dots from 0.05 to 0.1 mm in diameter. Scattered, large tube-like vertical structures may represent astrorhizae.

Remarks. The Victorian species from the Lilydale Limestone bears the closest resemblance to *T. altaica* Khalfina, 1968a, from the Lower Devonian succession near the mouth of the Solneshnaya River in the Altai Mountains. This latter species has 7 to 9 laminae in 2 mm, short ring pillars with diameters from 0.16 to 0.24 mm, and scattered dissepiments. The astrorhizae, described by Khalfina (1968a) as including canals in vertical rows and within interlaminar spaces, appear to be markedly more completely developed in *T. altaica* than the equivocal astrorhizal structures of *T. calamosa. T. tubulipilata* Khalfina, 1968a, also from the Lower Devonian of the Altai region, has more closely spaced laminae (9–13 in 2 mm) and apparently longer, superposed ring-pillars.

Genus Dendrostroma Lecompte, 1952

Type species. Idiostroma oculatum Nicholson, 1886b.

Remarks. This genus was introduced by Lecompte (1952) to accommodate dendroid to cylindrical forms previously assigned to *Idiostroma* but differing from members of that genus in having pillars chiefly confined to interlaminar spaces. Stearn (1966) noted the internal structure of *Dendrostroma* to be in some respects comparable to that of *Stromatoporella* or *Stictostroma*.

Dendrostroma? sp.

Figs 17E–F, 18A–C

non *Idiostroma oculatum* Nicholson 1886b: 101, figs 14–15.—Nicholson 1892: 225, figs 32–33, pl. 29, figs 8–11.
Idiostroma oculatum.—Ripper 1937b: 195, text-fig. 4, pl. 9, fig. 6.—Ripper 1938: 236.
non *Dendrostroma oculatum.*—Lecompte 1952: 320, pl. 61, fig. 1.

Material. Five specimens from the Lilydale Limestone at Mitchell's (Cave Hill) Quarry, Lilydale: NMV

Fig. 17. A–D, *Tubuliporella calamosa* (Ripper, 1933), Lilydale Limestone, Mitchell's (Cave Hill) Quarry: A, holotype NMV P141967 (*ex* NMV P13748), vertical section; B, holotype NMV P141966 (*ex* NMV P13748), tangential section; C, paratype A, NMV P141901 (*ex* NMV P13749), tangential section; D, paratype A, NMV P141984 (*ex* NMV P13749), vertical section showing irregular, ragged, external margin; A–C, × 10; D, × 5. E, F, *Dendrostroma?* sp., × 10, Lilydale Limestone, Mitchell's (Cave Hill) Quarry, Lilydale; E, NMV P141957 (*ex* NMV P13766), transverse section of outer part of lateral zone; F, NMV P141958 (*ex* NMV P13767), transverse section of axial column and inner lateral zone.
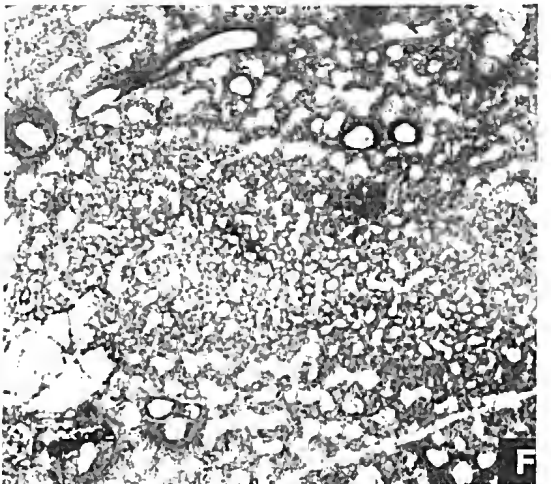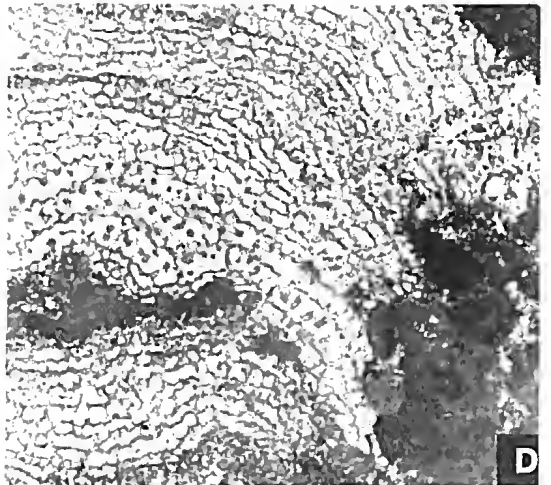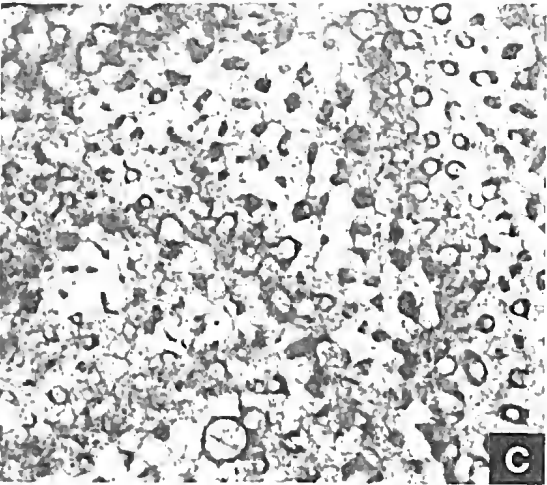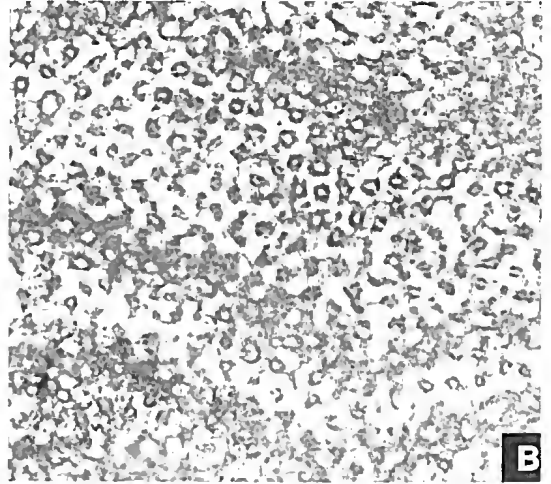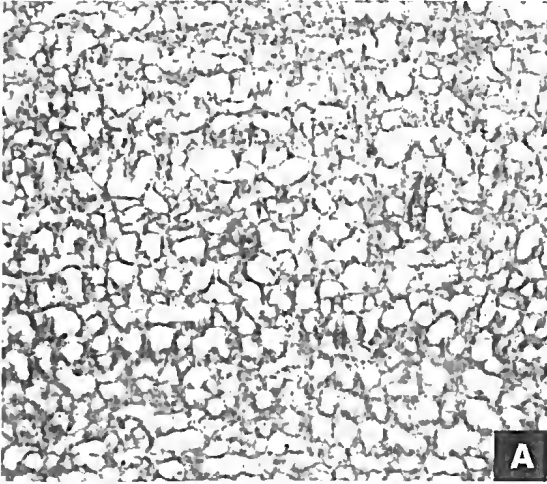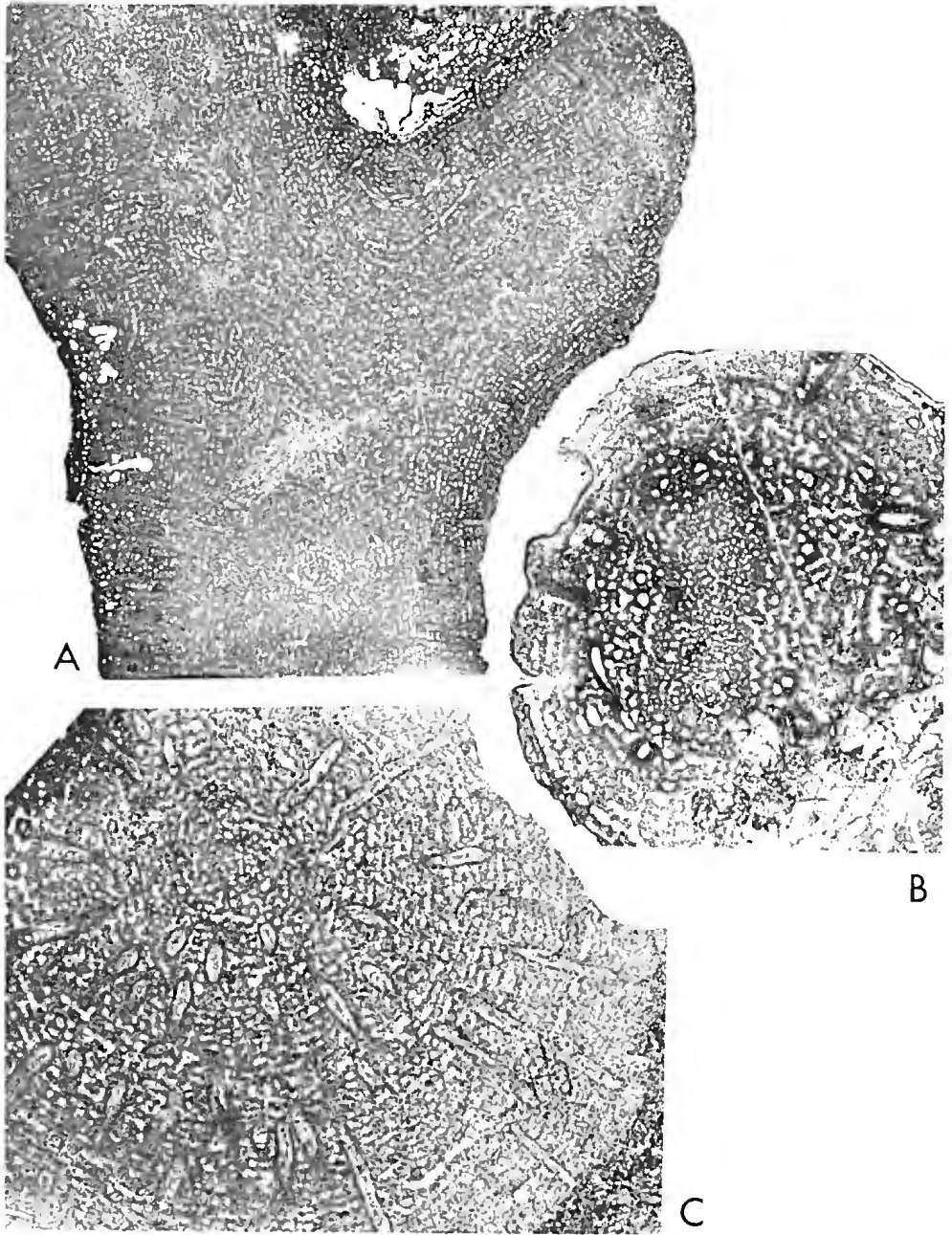
Fig. 18. A–C, *Dendrostroma*? sp., Lilydale Limestone, Mitchell's (Cave Hill) Quarry, Lilydale; A, NMV P136403 (*ex* NMV P13779), longitudinal section showing diehotomously branehing speeimen, × 2; photograph taken from eellulose aeetate-peel replica of acid-etehed speeimen rather than from thin section (as are all the others); the porous nature of the lateral margins of the speeimen prevented replieas made by this teehnique being entirely free of air bubbles (see espeeially midway along left margin of this illustration); B, NMV P141958 (*ex* NMV P13767), transverse seetion, × 5; for detail of axial eolumn see Fig. 17F; C, NMV P141916 (*ex* NMV P13779), transverse seetion, × 5.

P141956–57 (*ex* NMV P13766); NMV P141958 (*ex* NMV P13767); NMV P136403–10, P141916, P141980 (*ex* NMV P13779); NMV P141919, P141986 (*ex* NMV P13781); and NMV P136411–12, P141934, P142005–06 (*ex* NMV P13792).

Description. The cylindrical-dendroid skeleton is from 10 to 25 mm across and exhibits a clear differentiation into two parts: a finer-textured axial region, which is rarely associated with caunopore tubes; and a much larger lateral zone with the characteristic *Dendrostroma* morphology and abundant associated caunopore tubes (syringoporoid coral), from 0.4 to 0.7 mm in diameter. The axial region has the appearance of a fine, irregularly amalgamate meshwork, usually about 2.5 (rarely to 4.5) mm across. It is best developed in NMV P141958 and NMV P141916, and shows in transverse section a pattern of mainly rounded to irregular or, less commonly, labyrinthine spaces from 0.05 to 0.15 mm across between the darker skeletal elements (possibly mainly intersected coenosteles); in longitudinal section this axial zone of amalgamate skeletal material can be seen to be an upwardly domed extension of laminae and pillars (or coenosteles) of the lateral zone (Fig. 18A); under magnification the skeletal material shows in one small area a cellular microstructure and in another area a melanospheric microstructure. Other specimens (e.g. NMV P141956) exhibit the melanospheric microstructure, whereas others show a coarse-cellular structure, this latter possibly being of secondary origin.

The bulk of the skeleton is composed of the lateral zone. The laminae are thick, from 0.09 to 0.2 mm in thickness, arranged in concentric layers and spaced from 7 to 8 in 2 mm; there are a few breaks in the continuity of the laminae, suggesting pores, and these seen in transverse section are rounded and 0.1 to 0.2 mm across. Details of the laminae are limited because of the poor preservation, but in a few places a thin darker axial zone is seen, suggesting a tripartite layering. The darker infill may be bituminous matter and the layers above and below, at least in one specimen (NMV P141957), appear to be composed of transversely fibrous material. In transverse section of this same specimen (NMV P141956) a very pronounced darker speckled (?melanospheric) skeletal material is exhibited, each 'speck' being from 0.02 to 0.04 mm across. Pillars (or coenosteles) are solid, spool-shaped, typically less conspicuous than the laminae, and confined to interlaminar spaces; a few, however, are also seen to be superposed through two to

three laminae; in the lateral zone they seem best interpreted as pillars, from 0.1 to 0.2 mm across and with rounded to irregular cross section, but in the axial region they have a wall-like form enlosing rounded to labyrinthine spaces, confirming them as coenosteles. Dissepiments occur in larger gallery spaces, and in a few places where laminae are not continuous they may be superposed between pillars through an interval of 1 mm or so (through the equivalent of to 4 to 5 interlaminar spaces). No axial canal is present, and only a few traces of small branching astrorhizal canals have been confirmed in the lateral zone.

Remarks. The specimens are poorly preserved and consequently difficult to interpret. However, they should be excluded from the type species, *D. oculatum* from the Middle Devonian of Büchel, Germany, for none of them shows the well developed axial canal (see Lecompte 1952: 320, pl. 61, fig. 1). They may eventually prove to belong to a new taxon more closely allied to stromatoporids than to stromatoporellids (see description of *Stromatopora* sp. below), but this cannot be resolved with the available material.

Family HERMATOSTROMATIDAE Nestor, 1964

Genus **Amnestostroma** Bogoyavlenskaya, 1969

Type species. Syringostroma fedorovi Yavosky, 1929

Amnestostroma holmesae sp. nov.

Figs 19A–E, 31C–D

Syringostroma aff. *ristigouchense.*—Ripper 1937b: 181, pl. 8, figs 1–2.—Ripper 1938: 236.
non *Trupetostroma tenuilamellatum* Lecompte 1952: 225.

Material. Holotype (NMV P141860–64, *ex* MUGD 1619) and six paratypes (NMV P141983, *ex* NMV P13749; NMV P141915, *ex* NMV P13778; NMV P141976–77, *ex* NMV P13776; NMV P141865–66; NMV P141874; and NMV P141873) from the Lilydale Limestone at Mitchell's (Cave Hill) Quarry, Lilydale. An additional specimen (NMV P136332–33, *ex* NMV P136226) is from the Coopers Creek Limestone at Tyers Quarry.

Derivation of name. After Elizabeth A. Holmes (neé Ripper), pioneer Victorian stromatoporoid worker.

Diagnosis. A species of *Amnestostroma* characterized by an unequally thickened grid of stout, superposed pillars and thinner, tripartite laminae locally restricted in continuity to microlaminae between pillars, or disrupted by pores;

astrorhizae common and dissepiments apparently lacking.

Description. Skeleton is broadly mammillate and exhibits a few growth discontinuity surfaces, though latilaminae are not conspicuous; in places the skeleton has associated syringoporoids (up to 0.4 mm across), rugosans (up to 3 mm in diameter) and other large tube-like organisms (up to 1.7 mm across).

Vertical sections show a well defined grid of stout, superposed pillars and much finer laminae. Pillars are spool-shaped, commonly from 0.2 to 0.3 mm in diameter, and superposed for distances of at least 7 mm vertically. Laminae are tripartite with a thin lighter axial zone, and in places ordinicellular skeletal material intervening and bounded above and below by darker microlaminae; parts of the laminae between superposed pillars may be thinner, composed of a single dark layer, or continuity is broken by scattered transverse pores. Spacing of laminae is from 12 to 14 in 2 mm. The skeletal material of the pillars and outer parts of the laminae, where associated with bituminous matter, seems to be very finely melanospheric, suggesting a vaguely cellular texture (cellules from 0.01 to 0.02 mm) but in other places (perhaps because the thin sections of these areas of the skeleton are thicker) the material seems to be transversely fibrous. The microstructure of this skeletal material does not include larger vacuoles. Astrorhizae are widely scattered through the skeleton, both as growth-parallel canals, 0.15 to 0.20 mm in diameter, and as larger, upwardly turning, irregularly stacked, 0.3 to 0.4 mm wide, tabulated chambers, and seeming to link with partitioned vertical canalways up to 0.8 mm across.

In tangential section most pillars are rounded to irregular, from 0.2 to 0.25 mm in diameter, up to 9 spaced in 1 mm^2, but some are vermiform to meandriform and grade into meshworks towards the laminae. Laminae are represented by bands punctuated by abundant rounded pores from 0.1 to 0.2 mm in diameter. Microstructure of the pillars appears finely melanospheric, probably representing finely cellular (possibly clinoreticulate) skeletal material. Astrorhizae occupy interlaminar spaces as branching, wall-less canals up to 0.2 mm across.

Remarks. Ripper (1937a) assigned this Lilydale material to *Syringostroma* aff. *ristigouchense* (Spencer, 1884) on the basis that it could be distinguished from the species in its type locality and horizon in eastern Canada by having thinner, isolated pillars instead of vertical structures 'connected by whorls of radiating fibres', and by having thinner, less uniformly grouped laminae. Lecompte (1952) subsequently placed the Lilydale form questionably in his new species *Trupetostroma tenuilamellatum*. The transfer to *Trupetostroma* is not supported herein, for the Victorian species has pillars which are thick and non-vacuolate, the laminae are equally developed and tripartite, and the astrorhizae are not conspicuous, features more characteristic of the Late Silurian–Early Devonian genus *Amnestostroma*. This genus was regarded by Stearn (1990) as an early member of the Hermatostromatidae, whereas true *Trupetostroma*, also a representative of this family, enters the record only later, during Eifelian to late Frasnian time (Stearn 1993).

Amnestostroma holmesae differs from the type species *A. fedorovi* from the Upper Silurian of the Urals in exhibiting pillars only (no coenosteles), coarser skeletal elements, and more widely spaced laminae. *A. crassum* Webby & Zhen, 1993 from the Lower Devonian of New South Wales may also be distinguished by having more laterally continous, thicker and more widely spaced laminae (4 to 7 in 2 mm as compared with 12 to 14 in 2 mm in *A. holmesae*) and more widely spaced pillars.

Order STROMATOPORIDA Stearn, 1980
Family STROMATOPORIDAE Winchell, 1867

Genus **Pseudotrupetostroma** Khalfina & Yavorsky, 1971

Type species. Stromatopora pellucida var. *artyschtensis* Yavorsky, 1955.

Pseudotrupetostroma ripperae Webby & Zhen, 1993

Figs 19F, 20B–C

Fig. 19. A–E, *Amnestostroma holmesae* sp. nov., × 10, Lilydale Limestone, Mitchell's (Cave Hill) Quarry: A, holotype NMV P141861 (*ex* MUGD1619), vertical section; B, holotype NMV P141860 (*ex* MUGD 1619), tangential section; C, holotype NMV P141863 (*ex* MUGD 1619), tangential section; D, holotype NMV P141862 (*ex* MUGD 1619), vertical section; E, paratype NMV P141866, vertical section. F, *Pseudotrupetostroma ripperae* Webby & Zhen, 1993, NMV P141766 (*ex* MUGD 1612), vertical section, × 10, Buchan Caves Limestone, Heath's Quarry.
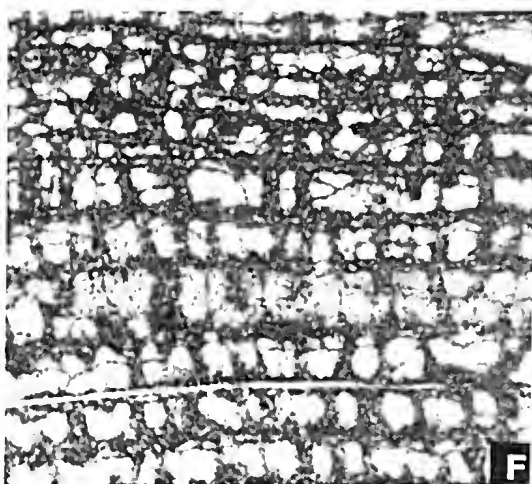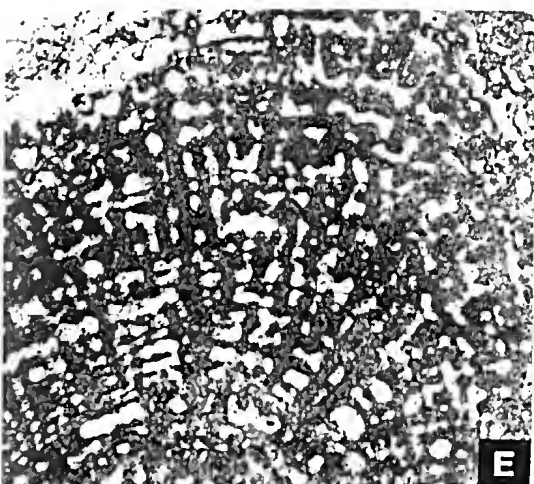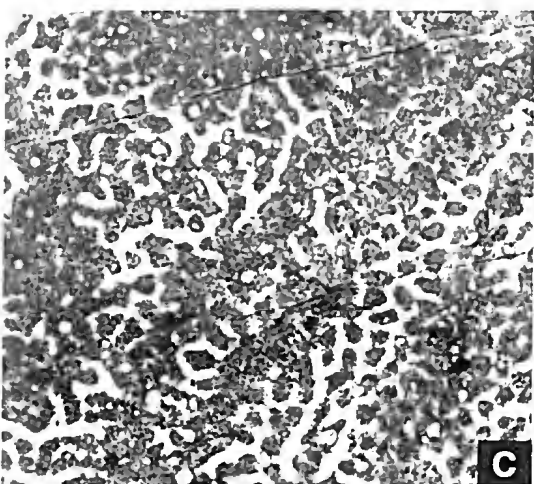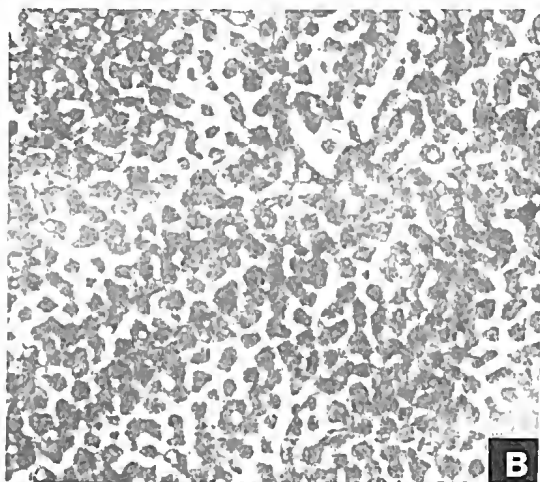
non *Hermatostroma episcopale* Nicholson 1892: 219, pl. 28, figs 4–11.
Hermatostroma episcopale.—Ripper 1937c: 29, pl. 5, figs 7–8.
Pseudotrupetostroma ripperae Webby & Zhen 1993: 340, figs 7A–F, 8C–D, 9A–B.

Material. Two well preserved specimens are from the Buchan Caves Limestone at Heath's Quarry; one (NMV P141765–66, *ex* MUGD 1612) was previously figured by Ripper (1937c), and the other (NMV P136297–98, *ex* NMV P136175) has associated caunopore tubes (0.5 mm in diameter).

Description. Coenostroms are gently undulating, relatively thick (up to 0.2 mm) and tripartite or locally cellular; less uniformly continuous, thicker lower and upper layers are separated by a continuous, thin, dark, apparently compact, median line (only 0.01–0.03 mm thick); spacing of coenostroms 4–7 in 2 mm. Pillars are similarly thick, spool-shaped elements which may be superposed or may be limited to single interlaminar spaces; range in diameter from 0.1 to 0.2 (commonly 0.15) mm and spaced from 0.1 to 0.25 mm apart (5–6 in 2 mm laterally). Mainly upwardly domed, blister-like dissepiments are common. Large vertical column of a possible astrorhizal system with septa-like radiating partitions in tangential section, up to 1.2 mm across; it is slightly offset from crest of broad, gently upwardly domed mamelon; there are few other traces of astrorhizal canals in the material under study. The coenostroms and pillars are coarsely cellular; cellules from 0.05 to 0.07 mm across. In tangential section rounded, irregular and vermiform coarsely cellular pillars are prominent. Coenostroms, where they are obliquely intersected in tangential sections, are obscurely melanospheric with vague traces of rounded pores about 0.15 mm across.

Remarks. The Heath's Quarry specimens are identical to the type specimens from the Jesse Limestone in central New South Wales. In the Museum of Victoria collections there are five other, less well preserved specimens from Heath's Quarry (NMV P136299–300, *ex* NMV P136176; NMV P136301–02, *ex* NMV P136177; NMV P136303–04, *ex* NMV P136178; NMV P136305–06, *ex* NMV P136179; NMV P136307–08, *ex* NMV P136180) and one specimen from Mitchell's (Cave Hill) Quarry at Lilydale (NMV P141935 and P142009, *ex* NMV P13793) labelled as *H. episcopale*, presumably identified by Ripper, but these are here only doubtfully assigned to *Pseudotrupetostroma ripperae*.

Pseudotrupetostroma buchanense (Ripper, 1937c)

Fig. 20A

Hermatostroma episcopale var. *buchanensis* Ripper 1937c: 32, pl. 5, figs 9–10.—Ripper 1938: 236.

Material. Of the two designated syntypes from the locality near Hicks's, Murrindal, probably from the Buchan Caves Limestone, NMV P141671–72 (*ex* MUGD 1602) is designated lectotype and NMV P141679–80 (*ex* MUGD 1603) paralectotype; two additional specimens from this locality are NMV P141660–61 and NMV P141683.

Comparative description. Ripper (1937c) argued that the Murrindal variant *buchanensis* had a sufficiently distinctive skeletal mesh—it was more irregular and coarser—to warrant separation from the species now recognized as *P. ripperae* Webby & Zhen. The former is therefore elevated herein to species rank, though the type material is somewhat poorly preserved, as is also the additional material housed in the Museum of Victoria (see above).

In vertical section laminae broadly undulate, spaced from 2.5 to 5 in 2 mm (some laminae more than 1 mm apart), tripartite with thin median dark line, and from 0.1 to 0.3 (commonly 0.2–0.3) mm in thickness. Pillars range in diameter from 0.08 to 0.25 mm and are rarely superposed; spaced from 4 to 5 pillars in 2 mm. Dissepiments common. No astrorhizae confirmed. Cellular microstructure presumably destroyed by recrystallization.

Compared with *P. ripperae*, *P. buchanense* has more widely spaced, more wavy to irregular laminae, and slightly more conspicuous mamelons. Both species are from the Buchan Caves Limestone, though *P. buchanense* may come from a higher stratigraphic level.

Fig. 20. A, *Pseudotrupetostroma buchanense* (Ripper, 1937c), lectotype NMV P141671 (*ex* MUGD 1602), vertical section, × 10, Buchan Caves Limestone near Hicks's, Murrindal. B, C, *Pseudotrupetostroma ripperae* Webby & Zhen, 1993, × 10, Buchan Caves Limestone, Heath's Quarry; B, NMV P141765 (*ex* MUGD 1612), tangential section; C, NMV P136297 (*ex* NMV P136175), vertical section. D–F, *Pseudotrupetostroma* sp., × 10, Murrindal Limestone, Rocky Camp Quarry; D, E, NMV P141730, vertical sections; F, NMV P141689, tangential-oblique section.
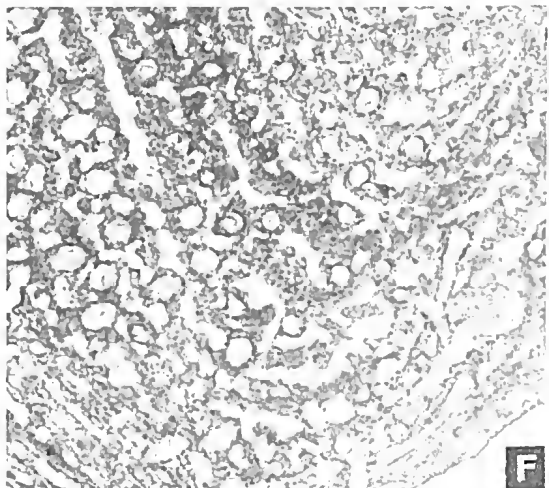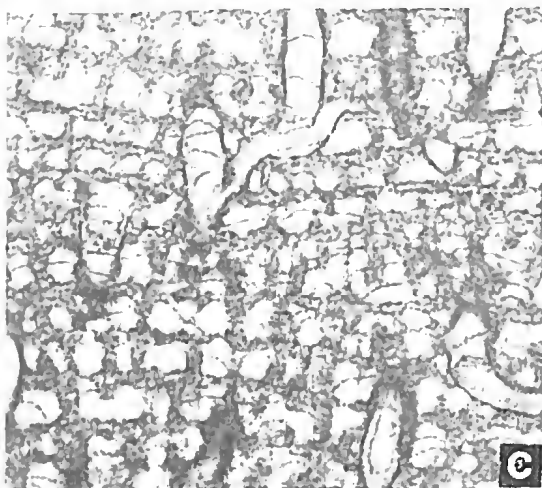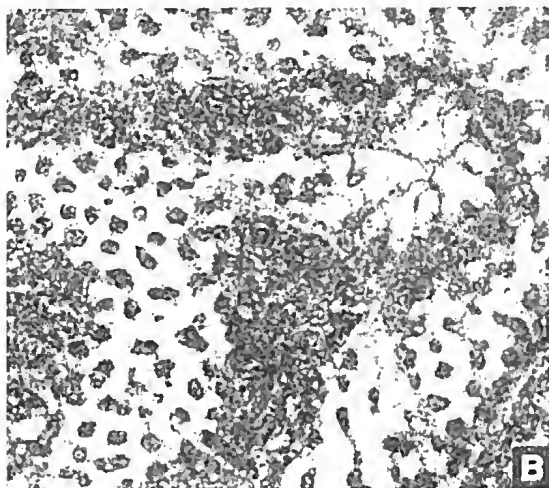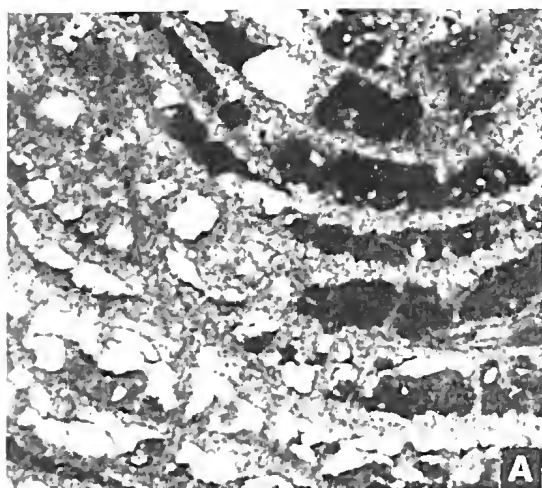
Pseudotrupetostroma sp.

Fig. 20D–F

Material. Three specimens (NMV P141730–32, NMV P141687–89 and NMV P141712) from the Rocky Camp Quarry, Murrindal Limestone, near Buchan.

Description. This species shows a grid-like structure of laminae with microlaminae and superposed coenosteles (in places discrete pillars); overall the surface is gently undulose. The skeleton is associated with syringoporoid corals (caunopore tubes) from 0.3 to 0.4 mm in diameter, and with the rugosan *Lyrielasma*. Latilaminae are not conspicuous, 9 mm or more thick.

Laminae are composed of layers of coarse cellular skeletal material between laterally more persistent, dark, thin microlaminae. Most commonly the coenostroms consist of one microlamina with an underlying row of cellules, or two (as paired) microlaminae with an intervening row of cellules, and locally an additional, less laterally complete underlying row of cellules; rarely even a third microlamina may occur where laminae are closely spaced. The laminae are spaced from 9 to 11 in 2 mm and are 0.06 to 0.08 mm thick, across paired microlaminae; individual microlaminae are 0.02 mm thick, and the cellules are from 0.03 to 0.04 mm across.

Vertical structural elements are commonly superposed, and are spool-shaped or inverted cone-shaped; the vaguely speckled appearance of these vertical elements suggests a now altered but originally coarse, cellular, skeletal material like, and at the tops in continuity with, the basal row of cellules of the overlying lamina. Vertical elements are rounded to vermicular in tangential section; from 0.12 to 0.2 (in extremes to 0.3) mm in diameter. Pores in laminae were not confirmed in tangential section. Vertical dissepimented astrorhizal canals (0.4 mm in diameter) are only prominently developed in the troughs of the skeleton, where they join radiating systems of growth-parallel canals, 0.2 to 0.3 mm wide.

Remarks. The Rocky Camp species is closely similar to *P. jessiensis* Webby & Zhen, 1993 from the Limekilns area of central New South Wales but exhibits more closely spaced laminae, 9 to 11 in 2 mm as compared with 5 to 8 in 2 mm in *P. jessiensis*, and the vertical astrorhizae have a peculiar association with troughs rather than with crests in the skeleton.

These Murrindal specimens are labelled in the Ripper collection of the Museum of Victoria as '*Stromatopora concentrica* var. *colliculata* Nicholson' but were not previously included by Ripper (1937c) in her description of that taxon from the Buchan area. That material is now referred to *Coenostroma* sp. (see below).

Genus Salairella Khalfina, 1961

Type species. S. multicea Khalfina, 1961.

Salairella lilydalensis (Ripper, 1937a)

Figs 21A–F, 22A–C, 31E

Stromatopora lilydalensis Ripper 1937a: 189, pl. 9, figs 1–2.—Ripper 1938: 236.
?*Parallelopora lilydalensis.*—Philip 1960: 153.—Philip 1962: 130.

Material. NMV P141924–25, P141992–93 (*ex* NMV P13785) is designated lectotype, and NMV P141961–62 (*ex* NMV P13768) is paralectotype; both are from the Lilydale Limestone at Mitchell's (Cave Hill) Quarry, Lilydale. The collection in the Museum of Victoria also includes NMV P141987–88 (*ex* NMV P13782), cited by Ripper (1937a: 190); NMV P141920–22 (*ex* NMV P13782), labelled in the collection as an additional syntype but not listed in Ripper's original description of the species; and four other specimens (NMV P141927–28 and P141997–98, *ex* NMV P13787; NMV P141868–70, *ex* MUGD 1621; NMV P141850–51; and NMV P141854–55); these also come from the Lilydale Limestone at the type locality. Two additional specimens (NMV P136309–10, *ex* NMV P136215; and NMV P136311–12, *ex* NMV P136216) are from the Coopers Creek Limestone at Tyers Quarry and should also be assigned to the species.

Description. In vertical sections the coenosteles are long and continuous, from 0.1 to 0.15 mm across, spaced from 7 to 8 in 2 mm, and typically diverge obliquely or join; intervening autotubes have similar dimensions, commonly from 0.1 to 0.15 mm (but in places up to 0.25 mm) across, similarly branch or join, and are crossed by horizontal to slightly upwardly domed dissepiments from 0.10 to 0.40 mm apart. Latilaminae com-

Fig. 21. Salairella lilydalensis (Ripper, 1937a), × 10; A, paralectotype NMV P141961 (*ex* NMV P13768), vertical section; B, lectotype NMV P141992 (*ex* NMV P13785), tangential section; C, lectotype NMV P141925 (*ex* NMV P13785), tangential section; D, NMV P141869 (*ex* MUGD 1621), vertical section; E, NMV P136311 (*ex* NMV P136216), vertical section; F, NMV P136312 (*ex* NMV P136216), tangential section; A–D, Lilydale Limestone, Mitchell's (Cave Hill) Quarry; E, F, Coopers Creek Limestone, Tyers Quarry.
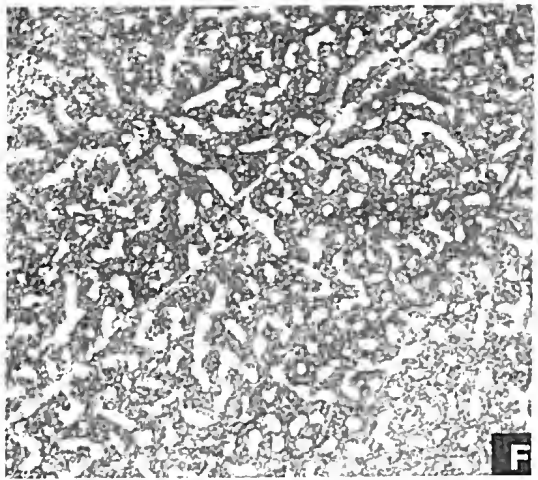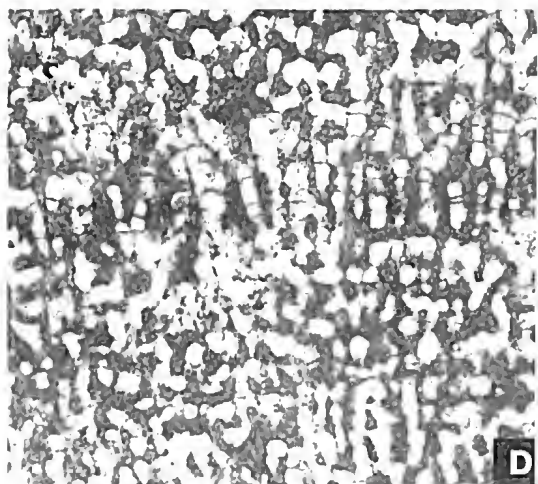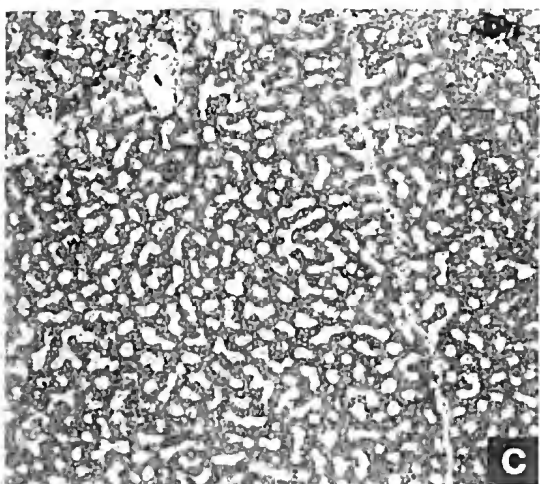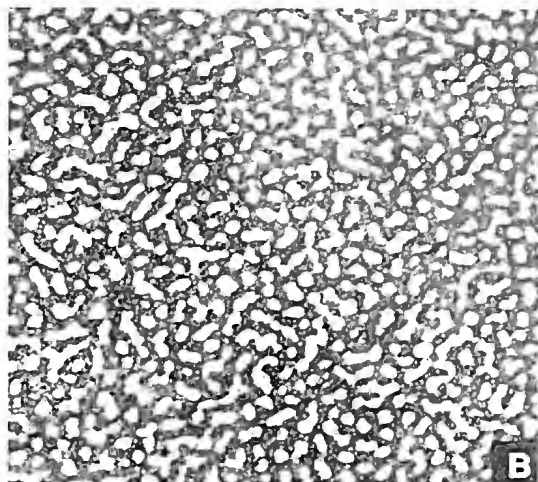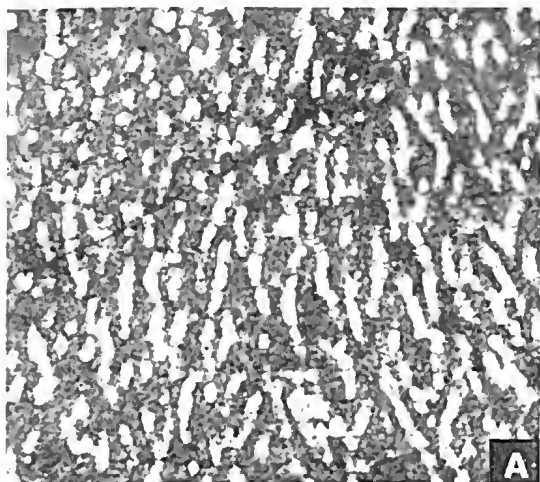
monly but not always present, up to 8 mm thick; locally differentiated by variably spaced pauses in growth or by thickening of skeletal material. Except at the bases or tops of latilaminae, coenostroms are commonly suppressed or impersistent, usually forming as offsets of similar thickness to the coenosteles, and linked horizontally or obliquely to them, at closely or widely spaced intervals. In one specimen (Fig. 21D) coenostroms are slightly more laterally extensive at levels in the skeleton other than at the bases and tops of latilaminae; rarely associated dissepiments may be aligned to form locally persistent microlaminae. Astrorhizae are composed of clusters of inwardly and upwardly directed, tabulated canals, from 0.15 to 0.20 mm in diameter. The microstructure is composed of cellular skeletal material, the cellules being from 0.03 to 0.06 mm in diameter and, commonly in better preserved areas of the skeleton, appearing in multiply stacked rows within coenosteles and associated coenostroms.

In tangential sections the coenosteles together with obliquely intersecting coenostroms form a mainly closed amalgamate network enclosing subcircular, irregular to vermicular autotubes, from 0.1 to 0.15 mm in width. Astrorhizae occur as small radiating and branching clusters with canals up to 2.5 mm in diameter, the clusters being spaced from 4 to 8 mm apart. In a few well preserved areas, the skeletal material bounding the autotubes is composed of two or three aligned rows of rounded cellules, with darker melanospheric dots preserved in the walls bounding some cellules.

Remarks. This species exhibits considerable internal variation. In tangential sections at some levels of the skeleton the distinctive closed network of autotubes is shown, but at other levels a more irregular to vermicular pattern (?coeno-tubes) is more suggestive of a species of *Syringostromella* than of *Salairella*. In vertical sections the pattern of upwardly joining and dividing coenosteles also seems more typical of *Syringostromella* than of *Salairella*, but for the present the species is retained in the latter genus. It differs from *Salairella prima* from the Middle

Devonian of the Omulevski Mountains of Siberia (Khromych 1971), and from similar material from the Lower Devonian (Emsian) of Arctic Canada (Stearn 1983) and the Jesse Limestone of central New South Wales (Webby & Zhen 1993), in having more obliquely dividing and joining coenosteles, and in having much smaller clustered astrorhizae.

Stromatopora Goldfuss, 1826

Type species. Stromatopora concentrica Goldfuss, 1826.

Stromatopora aff. polaris (Stearn, 1983)

Figs 5F, 23A–F, 24A

partim. *Stromatopora concentrica.*—Ripper 1937c: 24, pl. 4, figs 7–8 (not pl. 5, figs 1–2).
partim. *Stromatopora hüpschii.*—Ripper 1937c: 28 (not pl. 5, figs 5—6).
aff. *Ferestromatopora polaris* Stearn 1983: 551, figs 5A–D (*cum syn.*).
aff. *Stromatopora polaris.*—Stearn 1990: 507, fig. 3.8.
aff. *Stromatopora* cf. *Stromatopora polaris.*—Stearn 1990: 507, fig. 6.5, 6.6.
? *Stromatopora* sp.—Webby & Zhen 1993: 344, figs 10D–F, 12C–D.

Material. Specimens come from the following localities in the Buchan Caves Limestone: Heath's Quarry (NMV P141752–53, NMV P141775, NMV P141776–77); Martin Cameron's Quarry (NMV P141739), near Hicks's, Murrindal (NMV P141658–59, NMV P141662–63, NMV P141668, NMV P141673–74), and from Citadel Rocks, Murrindal River (NMV P141652–53, NMV P141656–57). Additional specimens are from the Murrindal Limestone at the Rocky Camp Quarry, near Buchan, including NMV P136326–27 (*ex* NMV P136223), NMV P136328–29 (*ex* NMV P136224), NMV P136330–31 (*ex* NMV P136225), NMV P141685–86, NMV P141719–20, and NMV P141721–22 (*ex* IUGD 1608).

Description. Specimens of this strongly latilaminate species may exhibit inter-or overgrowths of tabulate corals and/or calcareous algae. The closely spaced latilaminae are defined by abrupt changes or, less commonly, interruptions to growth; latilaminae are typically from 0.5 to

---

Fig. 22. A–C, *Salairella lilydalensis* (Ripper, 1937a), × 10, Lilydale Limestone, Mitchell's (Cave Hill) Quarry; A, NMV P141921 (*ex* NMV P13782), vertical section; B, NMV P141868 (*ex* MUGD 1621), tangential section; C, lectotype NMV P141993 (*ex* NMV P13785), vertical section. D–F, *Parallelopora ampla* sp. nov., × 10, Murrindal Limestone, Rocky Camp Quarry; D, holotype NMV P 136313 (*ex* NMV P136217), vertical section; E, holotype NMV P136314 (*ex* NMV P136217), tangential section; F, holotype NMV P136315 (*ex* NMV P136217), vertical section.
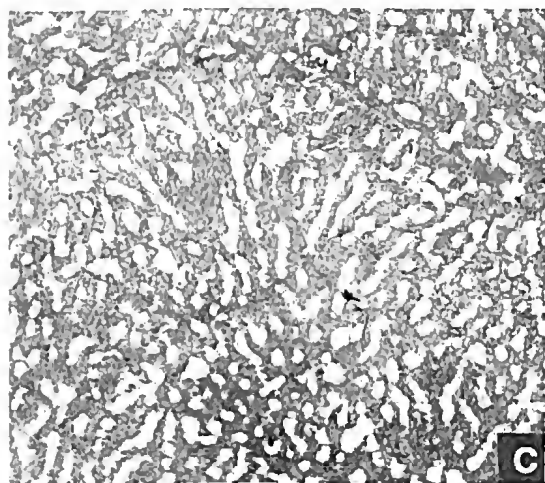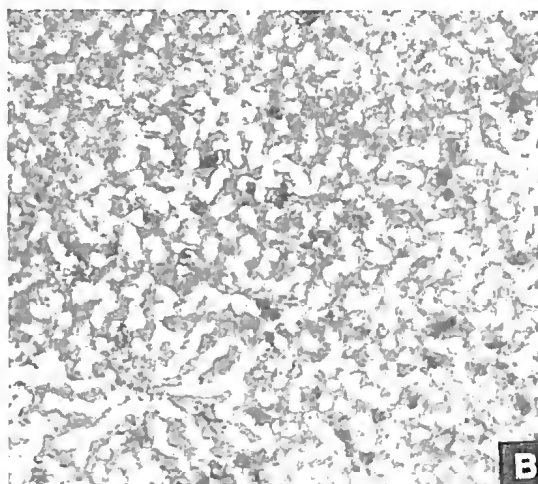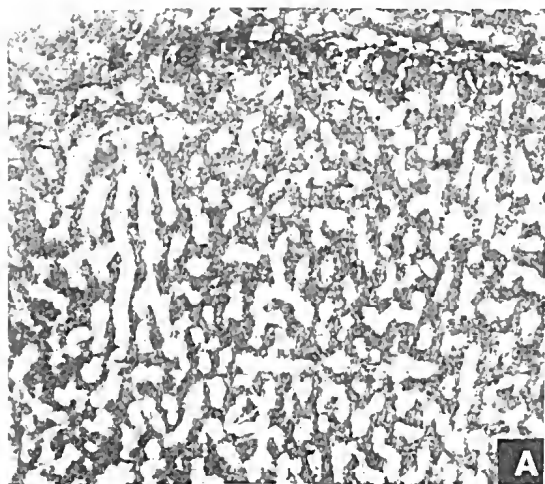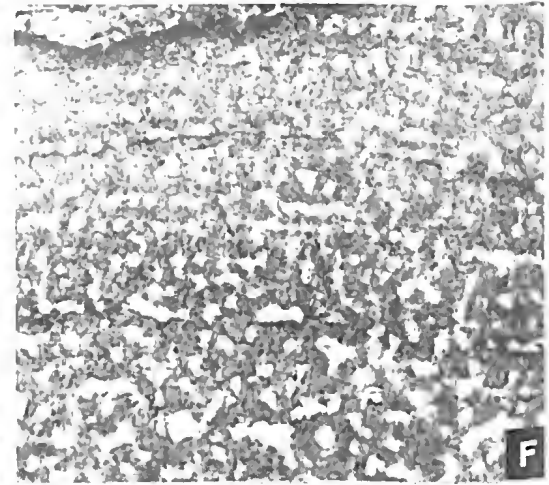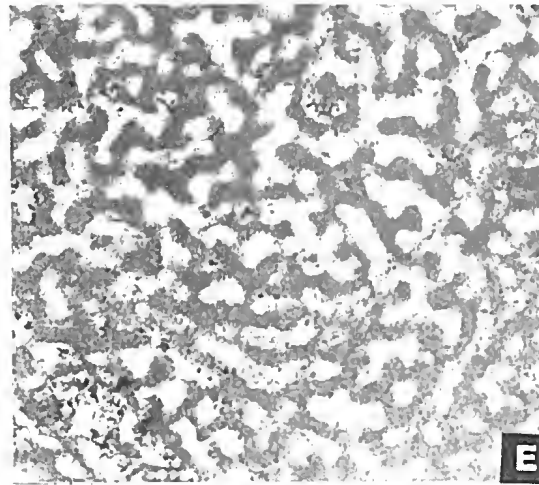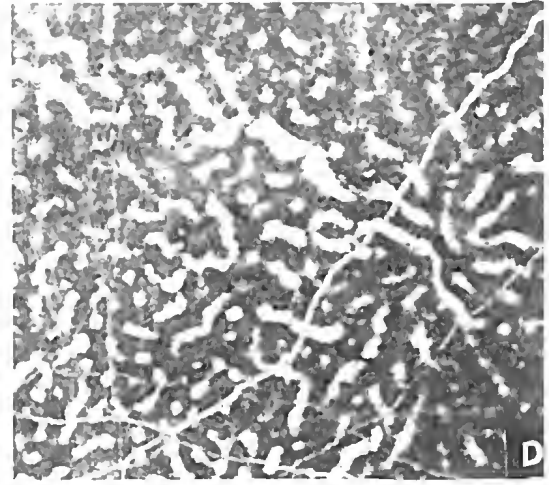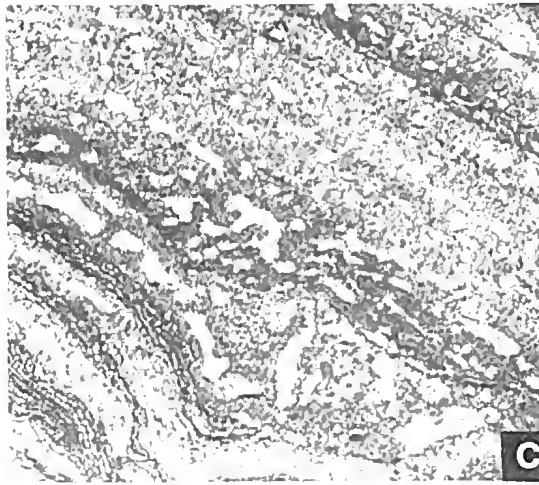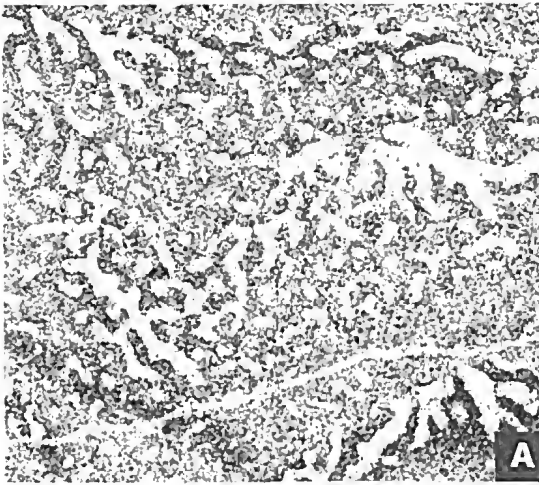
3 mm (in extremes to 6 mm) thick. Vertical sections show amalgamate skeletal material, locally developing a cassiculate meshwork, but short coenosteles predominate in isolated areas, and coenostroms are most prominent towards the bases and tops of latilaminae. The short coenosteles are from 0.1 to 0.2 mm in diameter and spaced 7 in 2 mm; the coenostroms are also from 0.1 to 0.2 mm thick but may be thickened (up to 0.3 mm) at the tops of latilaminae. This thickening is more pronounced in some specimens than in others. Dissepiments are regularly developed across intercoenostele (coenotube) spaces, also in more scattered occurrences crossing transversely elongated intercoenostromal spaces, and in a few places align to form incomplete microlaminae. The larger, transversely elongate and vertically aligned spaces are probably a part of astrorhizal canals.

In tangential sections the skeleton is a completely amalgamate network, the individual coenosteles being from 0.1 to 0.2 mm wide. Coenotubes are predominantly vermiform to meandriform but are locally rounded to irregular. Astrorhizal centres are spaced about 6 to 8 mm apart, with outwardly radiating and branching, wall-less canals from 0.15 to 0.25 mm wide. Well preserved specimens have a vaguely fine cellular microstructure.

Remarks. The Buchan specimens exhibit the latilaminate growth and cassiculate structure that is characteristic of the type species, *S. concentrica* Goldfuss, 1826 from the Middle and Upper Devonian of Europe and Asia (see recent discussions in Mistiaen 1985: 134 and Stearn 1990: 506), and of *S. polaris* (Stearn, 1983) from the Lower Devonian (Emsian) of Arctic Canada. Stearn (1990) noted the great range of variability and irregularity of structure of *S. polaris*, and similar characteristics are seen in the more-or-less age equivalent Buchan specimens now allied to this species. Better preserved specimens of *Stromatopora* sp. from the Jesse Limestone of central New South Wales (Webby & Zhen 1993) may also be conspecific but they are less finely and regularly latilaminate, and have more predominantly labyrinthine galleries than in typical representatives of *S. polaris*.

Stromatopora sp.

Fig. 24B–D

Stromatopora büchcliensis.—Ripper 1937b: 187, pl. 8, figs 9–10.—Ripper 1938: 236.—Philip 1962: 5.
Stromatopora büchcliensis var. *digitata.*—Ripper 1937b: 188, pl. 8, fig. 6, text-fig. 3A, B.—Ripper 1938: 236.

Material. Seven specimens (NMV P141906–08, P141946–48, *ex* NMV P13763; NMV P141963–64, *ex* NMV P13769; NMV P141975, *ex* NMV P13775; NMV P141926, P141994, *ex* NMV P13786; NMV P141936–37, P142010–1, *ex* NMV P13794; NMV P37642; and NMV P141913) from the Lilydale Limestone at Mitchell's (Cave Hill) Quarry.

Comparative description. The Lilydale material assigned by Ripper (1937b) to *Stromatopora buecheliensis* (Bargatzky, 1881) and to *S. buecheliensis digitata* Nicholson, 1891 is obscured by intergrowths of caunopore tubes of syringoporoid coral affinity, but despite this, it seems to comprise a range of growth forms from domical to digitate of one rather than two species. There is a possibility that the cylindrical forms previously referred by Ripper (1937b) to *Idiostroma oculatum* Nicholson, 1886b, and now classified herein as *Dendrostroma*? sp., may also be allied, but presently these seem better included tentatively within the stromatoporellids.

The fragmentary and comparatively poorly preserved skeletons of *Stromatopora* sp. show a few breaks in growth but latilaminae are not clearly evident. The skeleton is not dominated by either vertical or horizontal structural elements, though discrete short coenosteles from 0.1 to 0.2 mm across and impersistent coenostroms of similar dimensions are locally present; the chainlink, fence-like or cassiculate structure is, however, more conspicuously developed within the skeleton where not completely disrupted by intergrowths of caunopore tubes. The gallery spaces may be either closed with rounded to elongate outlines where the chainlink is completely formed, or more open, locally labyrinthine, at some other levels; in a few areas dissepimented coenotubes, from 0.1 to 0.2 mm across, are present.

Fig. 23. Stromatopora aff. *polaris* (Stearn, 1983), × 10; A, NMV P136327 (*ex* NMV P136223), tangential section; B, C, NMV P136326 (*ex* NMV P136223), vertical sections, note that Fig. 20C shows the species in intergrowth relations with a sheet-like alga; A–C, Murrindal Limestone, Rocky Camp Quarry; D, NMV P141662, tangential section, Buchan Caves Limestone near Hicks's, Murrindal; E, NMV P141776, tangential section; F, NMV P141775, vertical section; E, F, Buchan Caves Limestone, Heath's Quarry.
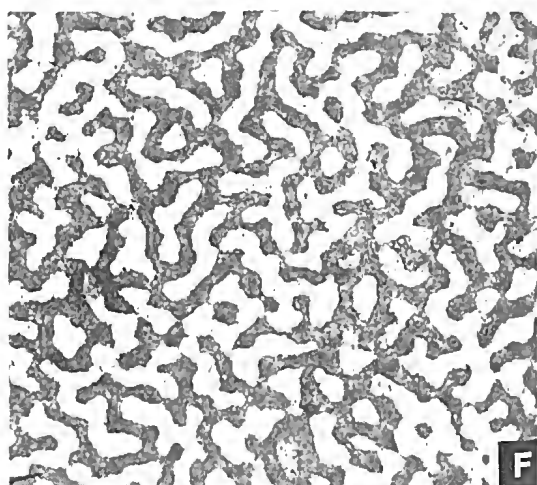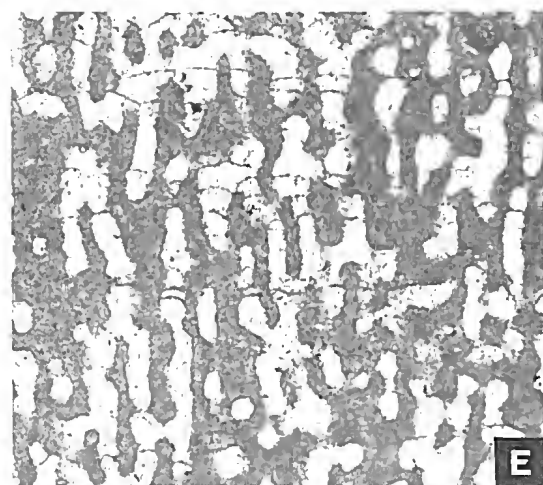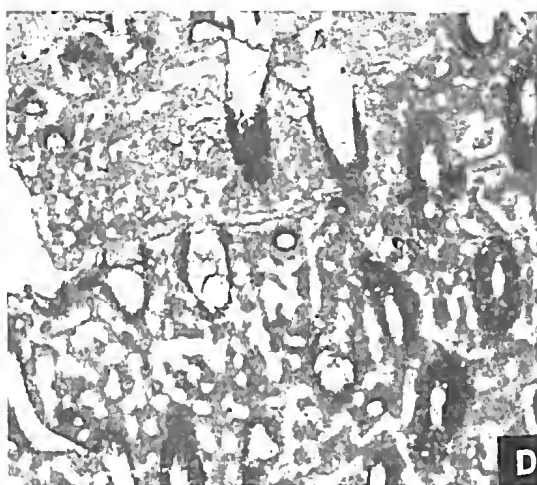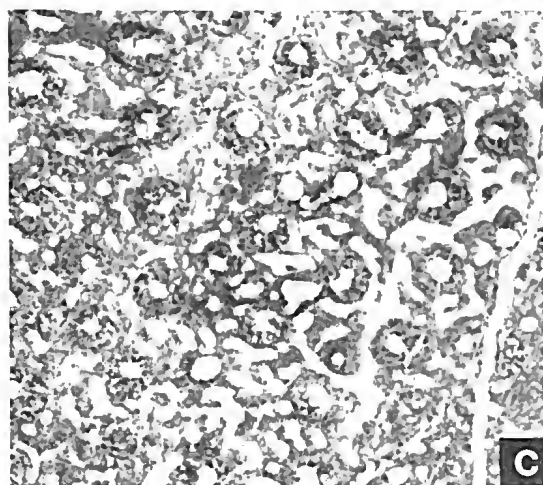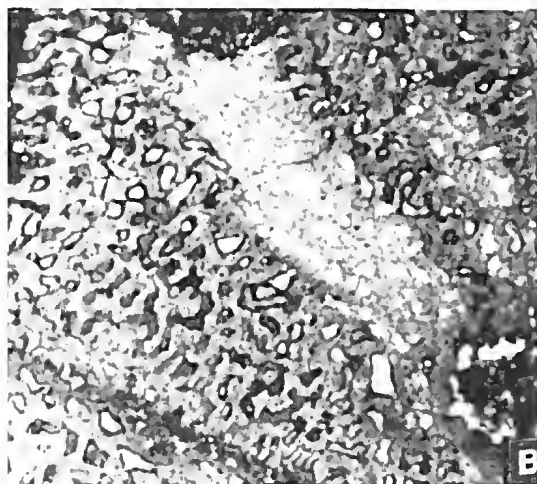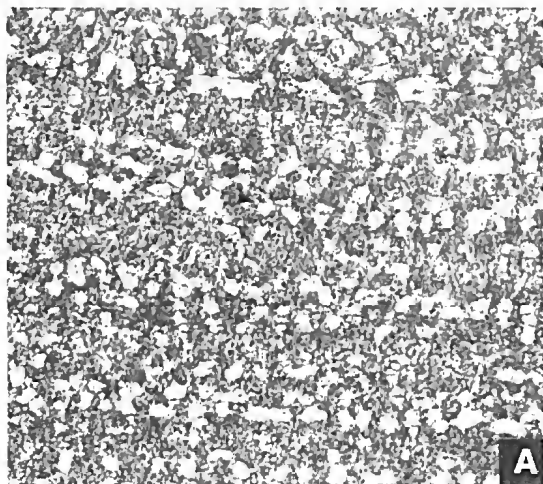
In tangential sections the network is amalgamate with most commonly labyrinthine to circular gallery spaces. Astrorhizae were not identified. Because of poor preservation it is not possible to confirm whether a cellular or other type of microstructure exists, but skeletal elements show a few vague traces of melanospheric texture.

Genus Syringostromella Nestor, 1966

Type species. Stromatopora borealis Nicholson, 1891.

Syringostromella zintchenkovi (Khalfina, 1961)

Figs 24E–F, 25A–C

Stromatopora aff. *hüpschii.*—Ripper 1937a: 186, pl. 8, figs 7–8.—Ripper 1938: 236.
non *Stromatopora hüpschii.*—Ripper 1937c: 28, pl. 5, figs 5—6.—Ripper 1938: 236.—?Teichert & Talent 1958: 20.
Stromatopora zintchenkovi Khalfina 1961: 327, pl. D3, fig. 1a, b.

Material. Four specimens from the Lilydale Limestone at Mitchell's (Cave Hill) Quarry, as follows: NMV P141930–31, P142003–04 (*ex* NMV P13790, previously figured material of Ripper 1937a), NMV P141917–18, P141981–82 (*ex* NMV P13780, previously allied to *S. lilydalensis*), NMV P141911–12, P141954-55 (*ex* NMV P13765), and NMV P141882–84 (previously labelled as *S. gemilis* Gortani).

Description. This species exhibits both laminar-domical and cylindrical growth forms. The individual branches of the latter range from 7 to 18 mm across and show rare growth bands not seen in the laminar-domical form. Internally the skeleton is composed dominantly of coenosteles, from 0.2 to 0.35 mm in diameter and spaced from 4 to 5 in 2 mm. Coenostroms are mainly offsets from the coenosteles; they are equally thick but lack lateral continuity; in a few places they occur successively in closely spaced intervals between adjacent coenosteles, resulting in a few oval to rounded galleries, from 0.2 to 0.3 mm across. Thin, long, convexly arched dissepiments also occur and may, at certain levels, align to form more laterally continuous microlaminae. Most of the remaining gallery space is open and meandriform because of the mainly

incomplete development of coenostroms and dissepiments. No astrorhizae have been confirmed and latilaminae are not clearly represented. Rows of cellules are in a few places vertically aligned parallel with the coenosteles and may, like a series of flow lines, curve into subhorizontal alignments at levels of successive coenostroms.

In tangential section the coenosteles and associated offsets form a vermiform to loosely labyrinthine network; only in a few areas is the maze-like network closed off with smaller rounded coenotubes from 0.2 to 0.3 mm across. Within the 0.15 to 0.3 mm wide coenosteles in the network, two or three rows of rounded to more elongate cellules are common; individually the cellules range from 0.03 to 0.05 mm (in extremes to 0.1 mm) across.

Remarks. The spacing of coenosteles, the width of structural elements, the nature of the dissepiments and their alignment at certain levels to form microlaminae, and the character of the labyrinthine networks in tangential section are all consistent with Khalfina's (1961) original description and illustrations of *S. zintchenkovi* from the Lower Devonian of Salair, southwestern Siberia. The significance of the Victorian specimens having areas of the skeleton with more open spaces (galleries and coenotubes) is difficult to assess until the limits of variation in the species are better understood.

Syringostromella cf. labyrinthea Stearn, 1990

Figs 25D–F, 32C

partim. *Stromatopora concentrica.*—Ripper 1937e: 24, pl. 5, figs 1–2 (not pl. 4, figs 7–8).
partim. *Stromatopora hüpschii.*—Ripper 1937c: 28, pl. 5, figs 5–6.
Syringostromella labyrinthea Stearn 1990: 507, figs 5.1, 5.2, 7.5, 7.6, 8.5 (*cum.syn.*)

Material. Three specimens from the Buchan Caves Limestone: two (NMV P141784–88, *ex* MUGD 1615; and NMV P141793) from Heath's Quarry, and one (NMV P141654–55, *ex* MUGD 1601) from Citadel Rocks, Murrindal River.

Description. Skeleton has latilaminae ranging from 1.5 to 8 mm (in extremes to 12 mm) in

---

Fig. 24. A, *Stromatopora* aff. *polaris* (Stearn, 1983), NMV P136329 (*ex* NMV P136224), vertical section, × 10, Murrindal Limestone, Rocky Camp Quarry. B–D, *Stromatopora* sp., × 10, Lilydale Limestone, Mitchell's (Cave Hill) Quarry; B, NMV P141964 (*ex* NMV P13769), tangential-oblique section; C, NMV P141906 (*ex* NMV P13763), tangential section; D, NMV P141907 (*ex* NMV P13763), vertical section. E, F, *Syringostromella zintchenkovi* (Khalfina, 1961), × 10, Lilydale Limestone, Mitchell's (Cave Hill) Quarry; E, NMV P141931 (*ex* NMV P13790), vertical section; F, NMV P141930 (*ex* NMV P13790), tangential section.

thickness; one specimen (NMV P141784–85) is intergrown with a specimen of *Pseudotrupetostroma ripperae*. In vertical section the coenosteles are prominent, thick and vertically continuous in the more broadly laminate parts of the skeleton (apparently shorter where the growth banding is more closely spaced); coenosteles are from 0.15 to 0.20 mm across and spaced from 6 to 7 in 2 mm. Coenostroms are represented mainly as local horizontal to oblique offsets from coenosteles, although at bases and tops of latilaminae they may be more continuous; they have a thickness equal to or less than that of the coenosteles. Coenotubes may be represented as vertically aligned, open labyrinthine spaces or may be locally closed where successive coenostrom offsets are developed; these latter are rounded to oval, from 0.13 to 0.2 mm across; in a few other areas, particularly towards the bases or tops of latilaminae where the coenosteles are less continuous, the gallery spaces may be transversely elongate. Astrorhizae occur in a few places in clusters of upwardly and inwardly tapering, tabulated canals, from 0.15 to 0.25 mm across. Scattered dissepiments occur at some levels in gallery spaces and may in rare instances form more continuous though poorly developed microlaminae.

Coenosteles form a distinctive vermiform to meandriform amalgamate network in tangential section, although throughout most of the skeleton there are also associated smaller closed subcircular to irregular coenotubes. The coenosteles are mainly from 0.1 to 0.2 mm across, and the coenotubes are of similar dimensions (0.15 to 0.18 mm). The coenosteles have a microstructure composed of 2 to 3 rows of cellules, and in better preserved areas of the skeleton the walls of the cellules appear to exhibit darker 'melanospheric' dots, possibly representing micropillars (but this cannot be confirmed in available vertical sections). The rounded cellules are of variable size, from 0.03 to 0.07 mm across. Up to four (or five) 'melanospheric' dots seem to occur around the periphery of individual cellules, and they are approximately 0.02–0.03 mm in diameter. Large radiating and branching astrorhizal structures are exhibited, with centres

about 3 to 4 mm across and spaced 15 mm apart; they exhibit long, sinuous canals from 0.18 to 0.3 mm wide.

Remarks. This species from Buchan has a finer texture and better preserved microstructures than in the Lilydale occurrences of *S. zintchenkovi*. The material is only provisionally assigned to *Syringostromella labyrinthea*, originally described from allochthonous limestones in the Lower Devonian of Arctic Canada, for the following reasons. First, though the spacing and thickness of coenosteles is very similar, they are apparently less vertically persistent (though this may be due to local variation related to the orientation of vertical sections) and, secondly, the coenostroms are seemingly at least locally more laterally extensive. Thirdly, the astrorhizae are more conspicuous, with upwardly-directed, tabulated astrorhizal canals in vertical sections of the Buchan specimens. Fourthly, latilaminae are clearly defined in the Buchan material but not recorded from the Canadian types. Fifthly, the Buchan material is better preserved; it exhibits details of the cellular (original?) microstructure not seen in the Canadian types.

Family SYRINGOSTROMATIDAE Lecompte, 1951

Parallelopora Bargatzky, 1881

Type species. Parallelopora ostiolata Bargatzky, 1881.

Remarks. Stearn (1993) noted that *Parallelopora* is distinguished by its coenosteles having a coarsely microreticulate microstructure and, in tangential section, mostly joining to form autotubes. The genus has hitherto been regarded by Stearn as restricted to the Middle Devonian, but the species described below extends the range down into the Emsian.

Parallelopora ampla sp. nov.

Figs 22D–F, 31F, 32A–B

Material. Holotype (NMV P136313–15, *ex* NMV P136217), two paratypes (NMV P136316–17, *ex* NMV P136218; NMV P136318019, *ex* NMV

Fig. 25. A–C, *Syringostromella zintchenkovi* (Khalfina, 1961), × 10, Lilydale Limestone, Mitchell's (Cave Hill) Quarry; A, NMV P142003 (*ex* NMV P13790), vertical section; B, NMV P141981 (*ex* NMV P13780), tangential section; C, NMV P141954 (*ex* NMV P13765), vertical–oblique section. D–F, *Syringostromella* cf. *labyrinthea* Stearn, 1990, × 10, Buchan Caves Limestone, Heath's Quarry; D, NMV P141786 (*ex* MUGD 1615), vertical section; E, NMV P141785 (*ex* MUGD 1615), vertical section; F, NMV P141784 (*ex* MUGD 1615), tangential section.
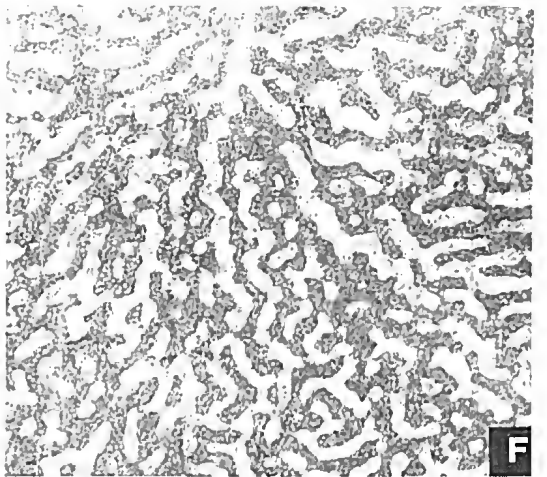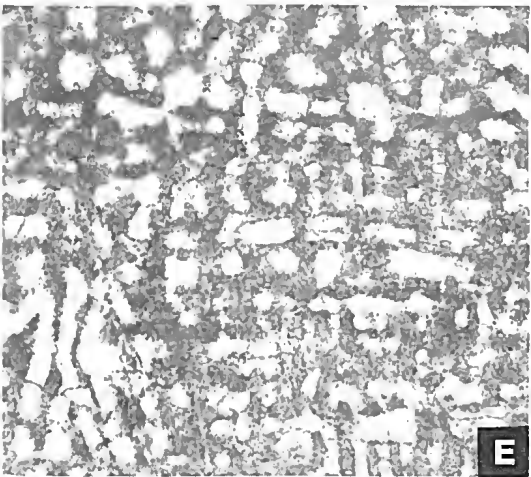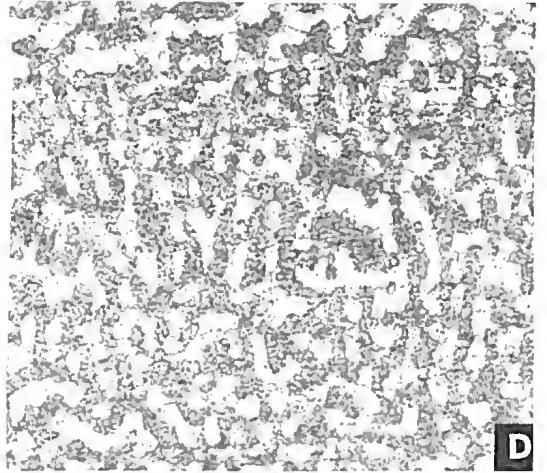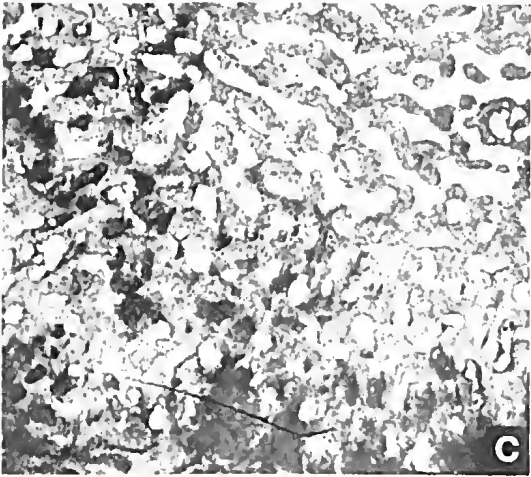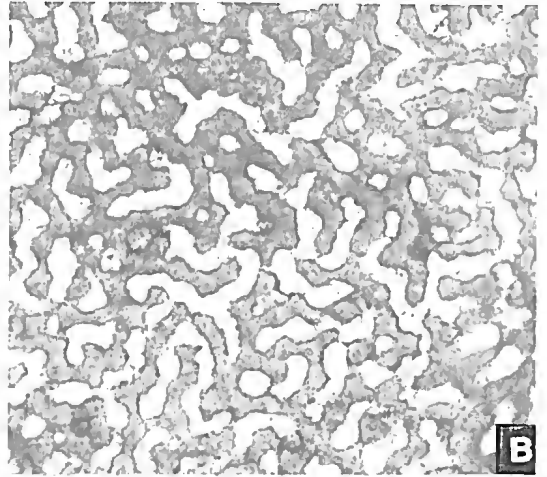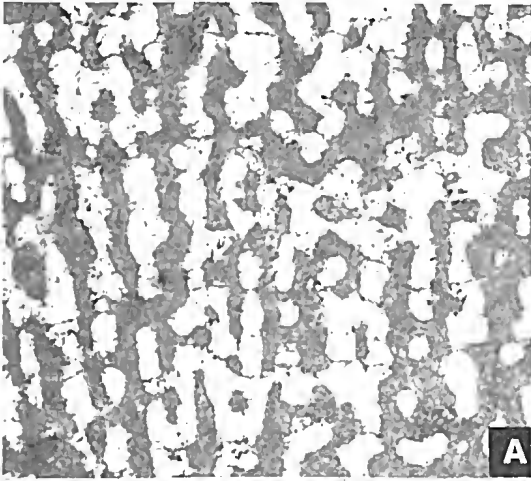
P136219), and three other specimens (NMV P136320–21, *ex* NMV P136220; NMV P136322–23, *ex* NMV P136221; and NMV P136324–35, *ex* NMV P136222), all from the Murrindal Limestone at the Rocky Camp Quarry, Buchan area.

Derivation of name. Latin *amplus*, large, alluding to the coarsely microreticulate skeletal material.

Diagnosis. Species of *Parallelopora* with long, erect coenosteles, 7 to 8 in 2 mm, each composed of 1 to 2 stacked rows of coarse cellules, individually 0.05–0.1 mm in diameter; coenostroms suppressed in favour of rows of closely spaced, aligned dissepiments simulating microlaminae; autotubes and less common coenotubes occur; astrorhizae well developed; latilaminae not confirmed; no mamelons.

Description. Skeleton domical; specimens with a maximum height of 270 mm and diameter of 750 mm. In vertical section the low domal skeleton has strongly developed vertical coenosteles from 0.1 to 0.15 mm in diameter, and spaced from 7 to 8 in 2 mm, with abundant horizontal to gently arched, closely spaced dissepiments crossing intercoenostele spaces, from 0.1 to 0.3 mm apart; in places these may be aligned to form microlaminae. The coenostroms are comparatively less prominent, rarely linking more than two or three coenosteles at a particular level. The most distinctive feature of this species is its coarsely cellular skeletal material, with most individual coenosteles being composed of only one or two rows of stacked large cellules, which may range in size from 0.05 to 0.1 mm across. A few slightly thickened bands are developed in parts of the skeleton but no well defined latilaminae.

In tangential section the coenosteles form a mainly closed, irregular network enclosing autotubes from 0.08 to 0.15 mm across, but locally the intercoenostele spaces are coenotubes of vermiform cross section. The coarse cellules tend to form in single or double rows within the coenostele network. Galleries occupy similar amounts of space to the skeletal elements, and astrorhizae form prominent clusters more than 3 mm across, spaced from 9 to 11 mm apart. The branching and radiating astrorhizal canals are from 0.15 to 0.25 mm wide.

Remarks. This species resembles the type species in the diameter and spacing of the coenosteles and in the pattern of aligned, closely spaced dissepiments forming microlaminae (Lecompte 1952, Galloway & St Jean 1957). However, the type species has better-defined latilaminae and the coenosteles show finer, more regularly aligned rows of cellules, commonly two to four rows to each coenostele, the individual cellules being 0.025 mm in diameter, as compared to *P. ampla* which has only one or two rows to each coenostele, the cellules being 0.05 to 0.1 mm in diameter.

Genus **Coenostroma** Winchell, 1867

Type species. Stromatopora monticulifera Winchell, 1866.

Coenostroma sp.

Fig. 26A–D

Stromatopora concentrica var. *colliculata.*—Ripper 1937e: 26, pl. 5, figs 3–4.—Ripper 1938: 236.

Material. Eight specimens from the Buchan Caves Limestone, Heath's Quarry, near Buchan: NMV P136334–35 (*ex* NMV P136181), NMV P136336–37 (*ex* NMV P136182), NMV P136338–39 (*ex* NMV P136183), NMV P136340–41 (*ex* NMV P136184), NMV P141751, NMV P141773–74, NMV P141778–79, NMV P141796–97. Ripper (1937e) previously figured NMV P141773 as pl. 5, fig. 3, and NMV P141774 as pl. 5, fig. 4).

Description. Surface is broadly mammillate with some astrorhizae. In vertical section thick coenostroms predominate and in most places form an amalgamate grid with the equally thick but less prominent and less extensive coenosteles; these latter are locally continuous across up to ten coenostroms. The coenostroms are of uneven thickness, commonly from 0.1 to 0.25 mm, and spaced from 6 to 8 in 2 mm; details of skeletal microstructure are limited by the poor preservation, but a few traces of thin, lighter and darker layers suggest microlaminae. Galleries tend to be rounded to slightly laterally elongate, from 0.1 to 0.2 mm across. In a few places, the normal, coarse, grid-like mesh is interrupted by a distinctive latilaminar discontinuity surface, with a dense, 0.1 mm thick basal layer and

Fig. 26. A–D, *Coenostroma* sp., × 10, Buchan Caves Limestone, Heath's Quarry; A, NMV P141751, vertical section; B, NMV P141797, tangential section; C, NMV P141774, tangential section; D, NMV P141773, vertical section. E, F, *Habrostroma tyersense* sp. nov., × 10, Coopers Creek Limestone, Tyers Quarry; E, holotype NMV P136342 (*ex* NMV P136185), vertical section; F, holotype NMV P136343 (*ex* NMV P136185), tangential section.
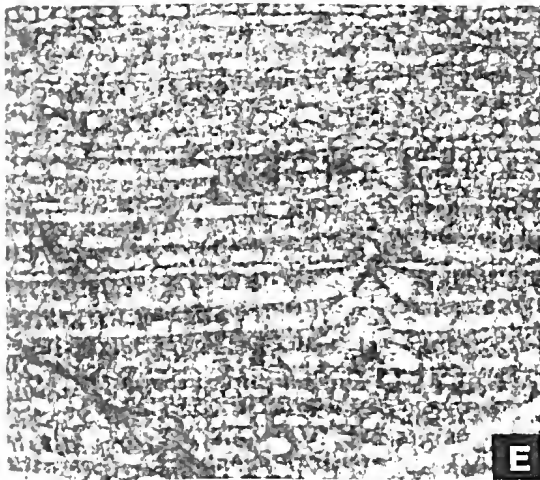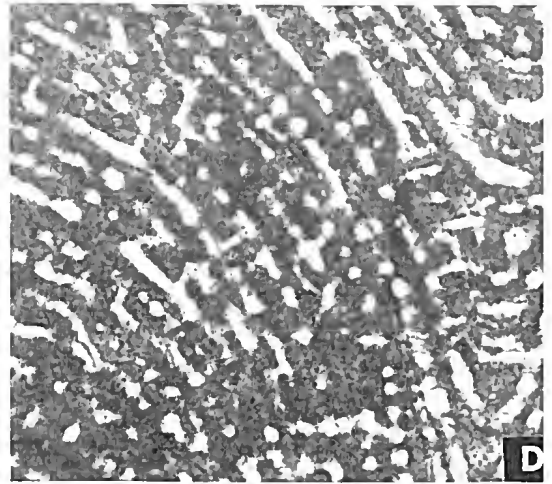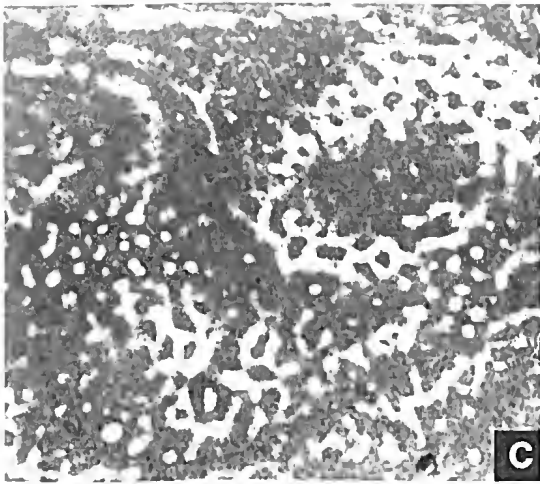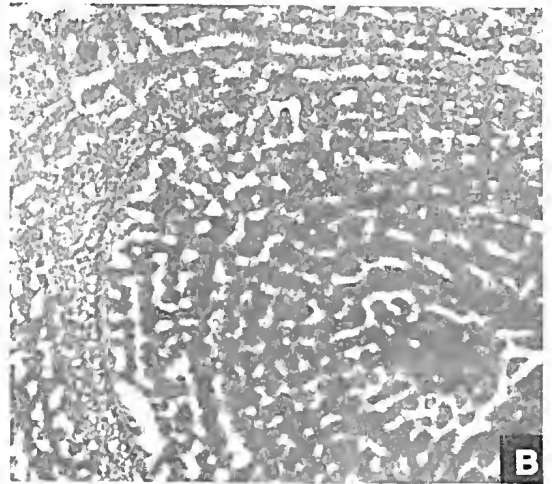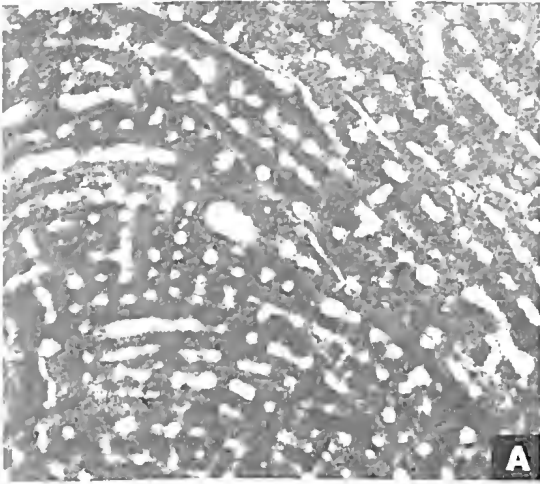
succeeding 0.5 mm thick unit of much finer amalgamate skeletal material.

In tangential section coenosteles form a vermicular to irregularly complete network, but there are also local areas of discrete pillars with rounded to irregular cross sections; these are from 0.1 to 0.3 mm (on average 0.2 mm) in diameter. Darker, concentric bands of skeletal material are coenostroms with a few rounded pores, from 0.1 to 0.2 mm across. Dissepiments are present in larger gallery spaces, commonly associated with discrete pillars, and may cross three or more successive interlaminar spaces in partitioning vertical astrorhizal canals or vertically elongated gallery spaces (?coenotubes). Astrorhizae comparatively small and scattered though the skeleton, with rare vertical canals up to 0.5 mm in diameter, and more common, branching, growth-parallel tubes from 0.15 to 0.3 mm wide.

Remarks. This species is based on a number of rather poorly preserved specimens. Despite additional collecting and preparation of new material, details of the finer structure and microstructure could not be further clarified. The species is therefore best left in open nomenclature.

These specimens resemble *Stromatopora teretiuscula* Yang & Dong, 1979 from the Fulong Member of the Donggangling Formation (Middle Devonian) of Ertang, Wu Xuan County, north-central Guangxi, south China. That species has similar dimensions and spacing of coenostroms and coenosteles (pillars), but these elements are less thickened, resulting in more prominent coenotubes. Also the astrorhizae are finer and less conspicuous.

Genus **Habrostroma** Fagerstrom, 1982

Type species. Stromatopora proxilaminata Fagerstrom, 1961.

Habrostroma tyersense sp. nov.

Figs 26E–F, 27A–E, 32D–E

Stromatopora foveolata.—Ripper 1937b: 185, text fig. 2A, B.—Ripper 1938: 236.

non *Stromatopora* aff. *foveolata.*—Ripper 1937c: 22, pl. 4, figs 5, 6.

Material. Holotype (NMV P136342–43, *ex* NMV P136185) and three paratypes (NMV P136344–45, *ex* NMV P136186; NMV P136346–47, *ex* NMV P136187; NMV P136348–50, *ex* NMV P136188) from the Coopers Creek Limestone, Tyers Quarry near Tyers. Three poorly preserved specimens (NMV P136351–53, *ex* NMV P136189; NMV P136354–55, *ex* NMV P136190; NMV P136356–57, *ex* NMV P136191) from the same horizon and locality are also included, as well as two other well preserved specimens (NMV P136358–59, *ex* NMV P136192; NMV P136360–61, *ex* NMV P136193) which have associated caunopore tubes and a minor morphological difference, namely, thinner coenostroms with fewer microlaminae, commonly the uppermost only being conspicuous (these latter forms possibly represent a separate variant). Three additional specimens, NMV P136402 (*ex* NMV P13771), NMV P141887–88, NMV P141909–10 and NMV P141949–50 (*ex* NMV P13764), from the Lilydale Limestone at Mitchell's (Cave Hill) Quarry, Lilydale, are also regarded as conspecific.

Two altered and sheared specimens, NMV P136362–63 (*ex* NMV P136195) and NMV P136364–65 (*ex* NMV P136196), from the limestone megaclast at Evans Quarry near Coopers Creek, are only doubtfully included. Another specimen (NMV P136366–67, *ex* NMV P136197) from the Waratah Limestone at the old limekilns site at Walkerville South is also only tentatively assigned since it exhibits a skeletal mesh close to the coarser end of the range of variability of the species. The Waratah specimen is associated with the symbiotic organism *Helicosalpinx* Oekentorp, 1969.

Derivation of name. After the type locality, Tyers Quarry.

Diagnosis. A species of *Habrostroma* with continuous, alternating couplets of porous coenostroms and intercoenostrom spaces (including coenosteles and galleries); couplets of variable thickness though retaining ratio of coenostrom thickness equal to, or less than, intervening gallery height; each coenostrom composed of one or more microlaminae (up to 4) and associated rows of microreticulate skeletal material; coenostroms spaced from 8 to 10 in 2 mm; astrorhizae well developed, with centres spaced 6–9 mm apart; microstructure cellular and microreticulate.

Fig. 27. A–E, *Habrostroma tyersense* sp. nov., × 10; A, NMV P136361 (*ex* NMV P136193), tangential section; B, paratype NMV P136349 (*ex* NMV P136188), vertical section; C, NMV P141887, vertical section; D, NMV P141888, tangential section; E, paratype NMV P136347 (*ex* NMV P136187), vertical section; A, B, E, Coopers Creek Limestone, Tyers Quarry; C, D, Lilydale Limestone, Mitchell's (Cave Hill) Quarry, Lilydale. F, *Atopostroma distans* (Ripper, 1937c), NMV P141782, vertical section, × 10, Buchan Caves Limestone, Heath's Quarry.
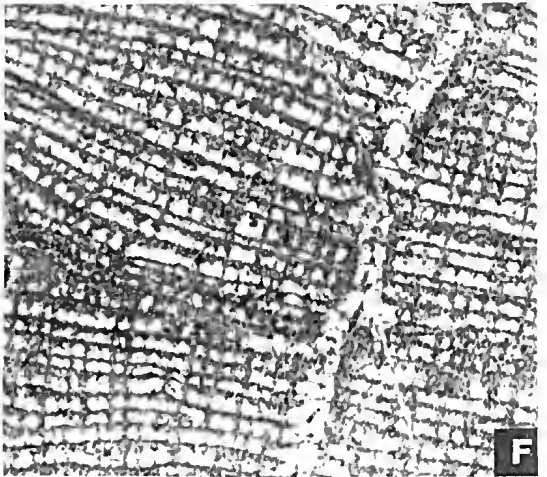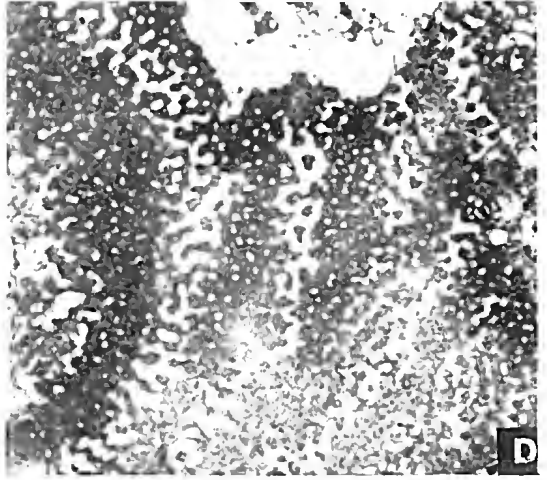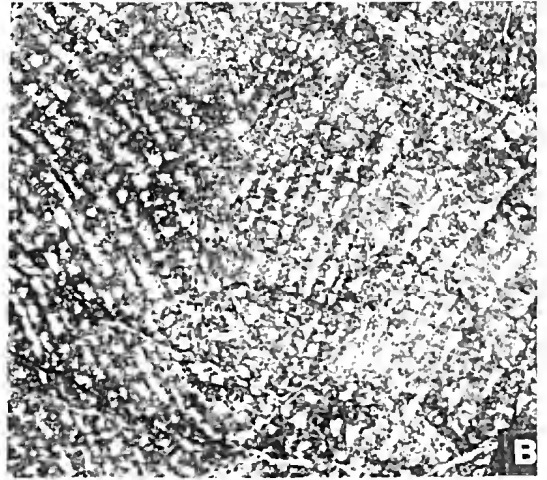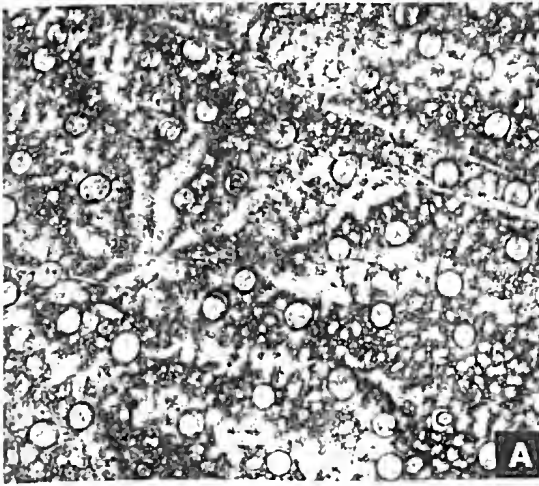
Description. The skeleton is laminar and the surface may be smooth or broadly mammillate with gently arched crests and moderately sharply folded troughs; and latilaminate, not with discontinuities but with alternating phases of thickened, closely spaced and more widely spaced coenostroms, in some specimens from 2 to 3 mm apart.

Coenostroms are continuous and of varying thickness, from 0.05 to 0.12 mm thick; spaced from 7 to 12 (most commonly 8 to 10) in 2 mm. Typically one or two, but in a few places up to four, microlaminae are present, with rows of small cellules intervening between the microlaminae; individual microlaminae are about 0.02 mm thick. Traced laterally one coenostrom with four microlaminae divides into two coenostroms each with paired microlaminae.

Coenosteles typically confined between coenostroms but in some places superposed through up to six intercoenostromal spaces; they are upward-flaring between coenostroms, and from 0.9 to 0.15 mm (rarely to 0.2 mm) in diameter; they are spaced from 9 to 11 in 2 mm. Gallery spaces are commonly dome-like, rarely oval, and a few have associated dissepiments; galleries may occupy one-half to three-quarters of the intercoenostromal spaces (the rest is coenostromal skeletal material). Astrorhizae include growth-parallel canals up to 0.2 mm, with a few tabulae which join vertical clusters of canals that may contain superposed tabulae.

In tangential sections vertical elements range from rounded to irregular (pillars), to vermicular (coenosteles). Obliquely intersected coenostroms show very abundant, rounded to irregular and rarely dumbbell-shaped pores, from 0.05 to 0.12 mm in diameter and spaced about 22 to 25 in 1 mm^2; the rounded pores under magnification show darker, wall-like rims of skeletal material about 0.01 mm thick. Astrorhizae prominent, forming outwardly radiating and branching, wall-less canals from centres spaced about 6.5 to 9 mm apart; each centre has up to six radiating canals extending from a 1 mm wide, ring-like cluster of vertical tubes; the growth-parallel canals may be impressed into the undersurface of the succeeding coenostrom; in a few places the canals abut against the denser, adjacent coenostromal skeletal material. Microstructure is cellular and microreticulate, with somewhat irregularly-shaped cellules from 0.03 to 0.05 mm across, and also in a few places darker specks occur around the periphery of the cellules (up to five giving a polygonal appearance); these may represent micropillars, from 0.01 to 0.02 mm across.

Remarks. The Lilydale specimens, formerly assigned by Ripper (1937b) to *Stromatopora foveolata* (Girty, 1895), are closely similar to the Tyers material but not as well preserved; the specimens also have very slightly thicker coenosteles (nearer to 0.2 mm in diameter) than typical representatives from Tyers but still presumably within limits of intraspecific variability of the species.

Ripper (1937b) allied a specimen from the Murrindal Limestone in the Rocky Camp Quarry of the Buchan district to the form she described as *Stromatopora foveolata* from Lilydale. She noted that it exhibits a somewhat coarser and more thickened skeletal mesh. This Rocky Camp specimen (NMV P141725–27, *ex* MUGD 1609) probably belongs to a second, stratigraphically slightly younger species of *Habrostroma*.

This well preserved species has the cellular and microreticulate microstructure of *Habrostroma* (akosmoreticular microstructure of Stock 1989), as shown in Fig. 31E, and it also seems clearly distinct from other described species of the genus. It most closely resembles *Habrostroma astrorhizoides* (Birkhead, 1967) from the lower part of the Cedar City Formation (Eifelian) in Missouri (Birkhead 1986), with similar spacing of vertical structural elements, cellular microstructure and astrorhizae, but it has a less regular alternation of coenostroms and open gallery spaces throughout the skeleton.

Habrostroma centrotum (Girty, 1895) from the Manlius Formation (Lochkovian) of New York, recently revised by Stock (1991), may also be compared, even though it is interpreted by Stearn (1993) as a representative of *Parallelostroma*. It has similar skeletal elements and proportions, with its regular and continuous coenostroms separated by gallery spaces. The gallery height is commonly equal to or greater than the thickness of the overlying coenostroms, as in *H. tyersense*. However, most specimens of *H. centrotum*, like the other Lochkovian species assigned to *Habrostroma* by Stock (1988, 1991), exhibit additional, localized, dissepiment-like microlaminae not seen in *H. tyersense*.

A species referred informally to *Habrostroma* from the Jesse Limestone (Emsian) of central New South Wales (Webby & Zhen 1993) shows little close resemblance to *H. tyersense* except in developing similar microreticulate skeletal material in the coenosteles.

Genus **Atopostroma** Yang & Dong, 1979

Type species. Atopostroma tuntouense Yang & Dong, 1979.

Remarks. Stearn (1983) and Webby & Zhen (1993) have summarised views on the interpretation of this genus.

Atopostroma distans (Ripper, 1937c)

Figs 27F, 28A—D

Actinostroma stellulatum var. *distans* Ripper 1937c: 12, pl. 2, figs 1–2.—Ripper 1938: 236.—Teichert & Talent 1958: 16.
Actinostroma cf. *distans.*—Flügel 1958b: 180.
Actinostroma (Actinostroma) distans.—Flügel 1959: 142.
Actinostroma stellulatum distans.—Flügel & Flügel-Kahler 1968: 403.
Trupetostroma cf. *ideale.*—Stearn & Mehotra 1970: 16, pl. 5, figs 1–2.
Atopostroma tuntouense.—Stearn 1983: 548, fig. 4E–H.
non *Atopostroma tuntouense.*-Stearn 1990: 496, figs 4.1, 4.2, 8.2.
Atopostroma distans.—Webby & Zhen 1993: 346, figs 11A–D, 12E.

Material. Holotype NMV P141754–57 (*ex* MUGD 1610) and eleven other specimens, NMV P136368–69 (*ex* NMV P136198), NMV P136370–71 (*ex* NMV P136199), NMV P136372–73 (*ex* NMV P136200), NMV P136374–75 (*ex* NMV P136201), NMV P136376–77 (*ex* NMV P136202), NMV P136378–79 (*ex* NMV P136203), NMV P136380 (*ex* NMV P136204), NMV P141767–68, NMV P141763–64, NMV P141782–83, NMV P141800–01), all from the Buchan Caves Limestone at Heath's Quarry.

Description. This latilaminate species shows the characteristic pattern of superposed pillars and laterally continuous, regular laminae. The pillars typically thicken upwards into overlying laminae and are from 0.10 to 0.15 mm thick; spaced from 8 to 9 in 2 mm. The laminae are of variable thickness, ranging from 0.07 to 0.15 mm in thickness; spaced from 7 to 12 in 2 mm; latilaminae may be defined by patterns of change in spacing and thickness of laminae and by interruptions of growth; they range from 2 to 14 mm in thickness; fork-like splays of individual laminae may occur with up to three microlaminae developed. Dissepiments are rare.

Astrorhizae are well developed and conspicuous, locally centred on crests but also commonly offset to the sides; composed of a regular series of single vertical columns spaced from 5 to 12 mm apart through the skeleton (individually traceable for up to 4 mm vertically), and each connecting into many (up to 13 counted) radiating and branching canals occupying interlaminar spaces; in the horizontal plane these individual stellate clusters may be up to 9 mm across; the columns are vertically traceable for up to 4 mm and are usually about 0.3 mm in diameter, and canals are wall-less and from 0.1 to 0.2 mm wide.

The shapes of pillars cut in tangential sections change markedly from the base to the top of an interlaminar space, from rounded to irregular outlines in the lower part, through elongate to curved and sinuous, to meandriform in the upper part, a part of an irregular network which merges into overlying laminae. Well preserved, obliquely intersected laminae show a random pattern of rounded pores, from 0.07 to 0.1 mm across, and much finer, rounded structures interpreted as cellules, about 0.01–0.03 mm across; this porous tissue is more clearly shown in the lower part of the lamina than in the denser upper part; at the top of the lamina there is an abrupt change into the overlying 'open' gallery, with again the widely spaced, rounded to irregular pillars.

Remarks. This species is recognized from the Buchan Caves Limestone at Heath's Quarry and from the Jesse Limestone (Emsian) of the Limekilns area, central New South Wales (Webby & Zhen 1993). Details of the listed synonymy have been discussed previously by Webby & Zhen (1993). *A. distans* differs from the type species, *A. tuntouense* from the Yujiang Formation (early Emsian) of Guangxi, south China, in having thicker laminae, thinner pillars with narrower spacing, and more prominent astrorhizae. The type species is recorded by Yang & Dong (1979) as having thin and compact laminae, 0.02–0.03 mm thick and spaced 6–7 in 2 mm (locally up to 9–10 in 2 mm); thick pillars, slightly widening upwards and superposed, 0.15–0.18 mm in diameter and spaced 6–8 in 2 mm; pillars appearing as irregular dots in tangential section, with 3–5 radial processes, merging into sharp pointed networks adjacent to laminae; diameter of cellules 0.01 mm and of vacuoles (pores) 0.02 mm; weakly developed astrorhizae, with canals 0.17–0.19 mm wide.

A. distans also occurs in the Blue Fiord Formation (early Emsian) of Arctic Canada. Stearn (1983) previously assigned the Blue Fiord specimens to the type species but they more closely resemble *A. distans* in respect to the thickened laminae, microlaminae and astrorhizae. Other material also included in *A. tuntouense* by Stearn
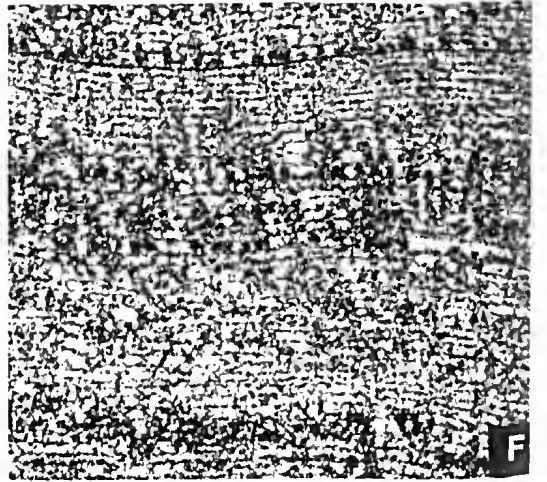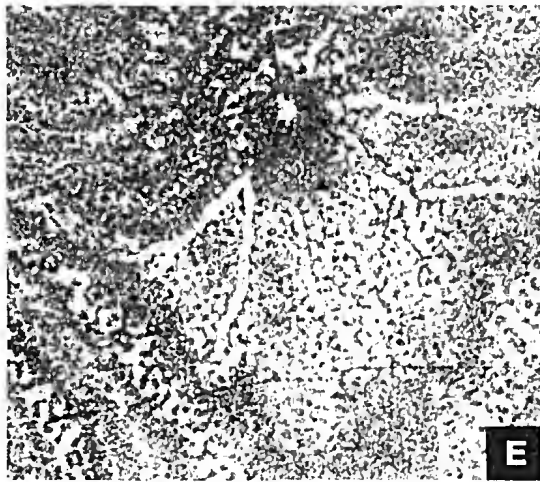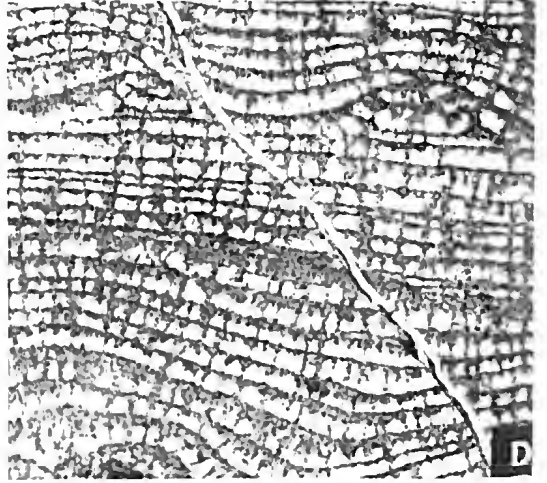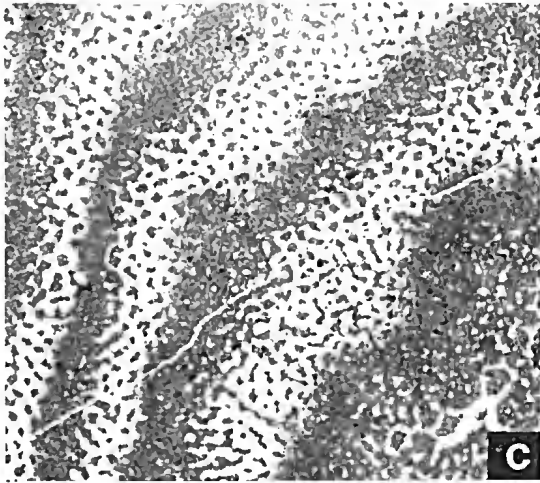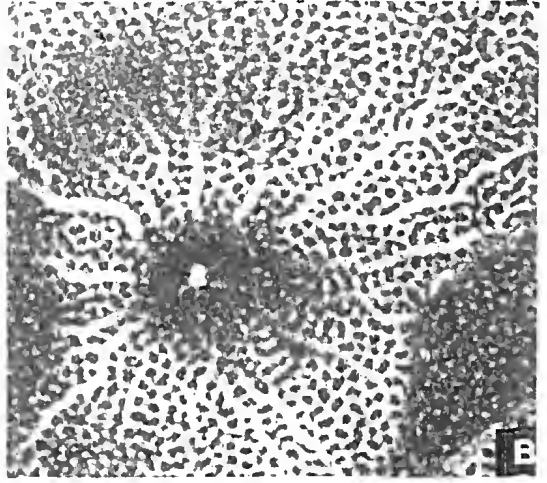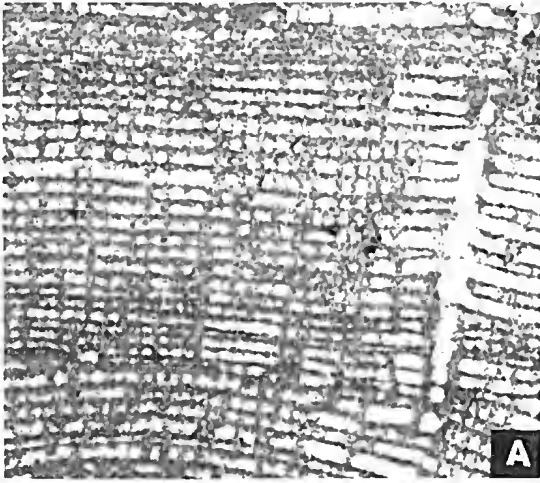
(1990), from allochthonous Early Devonian clasts in the Stuart Bay Formation of Arctic Canada, is markedly different, having much closer spacing of laminae (16 in 2 mm as compared with 7 to 12 in 2 mm of *A. distans*), and should probably be excluded from both named taxa.

Atopostroma flexuosum (Yavorsky, 1955) from the Eifelian of the Kuznetsk Basin, Russia, differs from *A. distans* in having thinner and more widely spaced laminae, and less conspicuously superposed and variably spaced, gently curved pillars.

Three additional specimens (NMV P136381–82, *ex* NMV P136207; NMV P136383–84, *ex* NMV P136208; NMV P136385–86, *ex* NMV P136209) from the Buchan Caves Limestone at Heath's Quarry are doubtfully included in the species because they are poorly preserved and show a more thickened (possibly secondarily altered), regular grid-like mesh of laminae and pillars, somewhat similar to the structure of *Gerronostroma*, and the laminae are slightly more closely spaced, from 9 to 14 in 2 mm.

Atopostroma sp.

Fig. 28E–F

Material. One specimen (NMV P136387–88, *ex* NMV P136210) from the Murrindal Limestone at Rocky Camp Quarry, Buchan area.

Comparative description. This finer species of *Atopostroma* is represented by only one specimen. It is conspicuously latilaminate (the latilaminae from 2 mm to more than 7 mm apart) and weakly mammillate (with domes spaced about 11 to 15 mm apart); it has regular, thin, laterally continuous laminae, and comparatively thickened and in many places superposed pillars. The laminae are closely spaced from 15 to 17 in 2 mm, and are 0.02 to 0.03 mm (sometimes to 0.05 mm) thick. The pillars are from 0.05 to 0.10 mm (commonly 0.07–0.08 mm) in diameter, and 0.10 to 0.15 mm apart (from 9 to 12 in 2 mm). Astrorhizae are very conspicuous in tangential section, with radiating clusters from 7 to 11 mm apart, and individual stellate, branching canals from 0.12 to 0.25 mm across;

these clusters are not always associated with mamelons.

Although this Murrindal species has the same spacing of laminae and pillars as in Stearn's (1990) Stuart Bay *Atopostroma* (doubtfully either *tuntouense* or *distans*), it differs markedly in other features, such as the thickness of pillars (0.07–0.08 mm in diameter in the Murrindal species, 0.15 mm in the Stuart Bay species) and astrorhizae (large and well developed in the Murrindal species, small and inconspicuous in the Stuart Bay species).

Genus **Columnostroma** Bogoyavlenskaya, 1972a

Type species. Coenostroma ristigouchensis Spencer, 1884.

Remarks. In terms of generic relationships, Stearn (1966) first commented that, based on its gross structure, *Syringostroma ristigouchense* (Spencer, 1884) was better placed in *Parallelopora*. However, Fagerstrom (1982, pl. 3, figs 7–8) retained the species in *Syringostroma*, although Bogoyavlenskaya (1972a) established the new genus *Columnostroma* based on *S. ristigouchense* as type species. *Columnostroma* is characterized by the presence of long, continuous, clinoreticulate and rounded pillars, thick coenostroms only locally persistent and interrupted by pores, and coenotubes with dissepiments (Stearn 1993).

Columnostroma clathratum sp. nov.

Figs 29A–F, 32F

Syringostroma aff. *niagarense.*—Ripper 1937b: 179, text-fig. 1.—Ripper, 1938: 236.

Material. Holotype, NMV P141922–23, P141990–91 (*ex* NMV P13784) and three paratypes, NMV P141932–33, P142007–08 (*ex* NMV P13791), NMV P141875–76, and NMV P37638, all from the Lilydale Limestone at Mitchell's (Caves Hill) Quarry, Lilydale.

Derivation of name. Latin *clathratus*, meaning latticed or screened.

Diagnosis. A species of *Columnostroma* with long, stout, microreticulate pillars forming an incipient network with thin, closely spaced,

---

Fig. 28. A–D, *Atopostroma distans* (Ripper, 1937c), × 10, Buchan Caves Limestone, Heath's Quarry; A, holotype NMV P141755 (*ex* MUGD 1610), vertical section; B, holotype NMV P141757 (*ex* MUGD 1610), tangential section; C, NMV P141783, tangential section; D, NMV P141782, vertical section. E, F, *Atopostroma* sp., × 10, Murrindal Limestone, Rocky Camp Quarry; E, NMV P136388 (*ex* NMV P136210), tangential section; F, NMV P136387 (*ex* NMV P136210), vertical section.

porous laminae or horizontal dissepiments (16–22 in 2 mm); latilaminae at least 10 mm thick, and scattered astrorhizae.

Description. Only a few discontinuity surfaces occur, and latilaminae are widely spaced, at least 10 mm thick; overall skeleton is laminar to weakly mammillate. Vertical sections composed of a grid with dominance of stout, long, spool-shaped, superposed pillars and less prominent, thin, closely spaced laminae. The pillars extend continuously through at least 8 mm vertically and do not branch; they are spaced from 8 to 9 in 2 mm and each is about 0.2 mm in diameter. Only in a few places are traces of a cellular, possibly a clinoreticulate, microstructure shown in the pillars.

Because of the comparatively poor preservation it is difficult to interpret the nature of laminae between the pillars; in the interspaces between the pillars they are most commonly thin, horizontal plates, apparently continuous, about 0.02 to 0.03 mm thick, and resembling microlaminae (or horizontal dissepiments), but in some other places they are thicker, though not laterally extensive layers, up to 0.1 mm thick. The spacing of laminae is from 16 to 22 in 2 mm. The interspaces between the pillars appear in a few areas of the skeleton more like coenotubes crossed by horizontal dissepiments but in most other areas like gallery spaces bounded by thicker laminae. Astrorhizal canals occupy transversely elongated gallery spaces, and are from 0.1 to 0.15 mm wide; they bend upwards to join one or more of the ring-like clusters of vertical canals (each 0.15 mm across) in various parts of the skeleton in tangential section.

Pillars have rounded to irregular outlines in tangential sections but tend to be more vermicular near intersections with laminae; they range from 0.15 to 0.2 mm in diameter and show a microstructure of cellules about 0.02 to 0.03 mm across. The laminae have abundant rounded pores from 0.08 to 0.15 mm (on average 0.1 mm) in diameter; from 14 to 20 in each 1 mm². Astrorhizae comprise branching and radiating, growth-parallel, wall-less canals from 0.12 to 0.2 mm in diameter; a few ring-like clusters of 2

to 5 vertical tubes, each from 0.15 to 0.2 mm in diameter.

Remarks. Compared with the type species, *C. ristigouchensis* from the Lower Devonian of New Brunswick, Canada (see Fagerstrom 1982, pl. 3, figs 7, 8), *C. clathratum* has a more densely fused skeletal structure, closer spacing of thin laminae, and more continuously linked networks of pillars and laminae with pores in tangential section. Relatively greater areas of the skeleton of the type species, as seen in tangential section, exhibit isolated, rounded pillars joined by radial processes (possibly these latter represent intersections with the blister-like dissepiments seen in vertical section). *C. gallowayi* (Fritz & Waines, 1956), from the Middle Devonian Upper Abitibi River Formation of Ontario, exhibits a closer resemblance to the Victorian species, with pillars of much the same dimensions and spacing, and a similar fused network pattern of pillars and laminae with pores in tangential section. However, *C. gallowayi* has very thin latilaminae (about 0.5 to 0.8 mm thick) and obscure, ill-defined laminae. None of the six other species assigned to the genus (Stearn 1993) is similar to *C. clathratum*.

Order AMPHIPORIDA Rukhin, 1938

Genus Stellopora Bogoyavlenskaya 1972b

? *Columdictyon* Dong & Wang 1982: 29–31.
? *Tianshanostroma* Dong & Wang 1984: 269.
? *Qinghaipora* Dong 1991: 75.

Type species. Amphipora intexta Yavorsky, 1957.

Remarks. Bogoyavlenskaya (1972b) established *Stellopora* with *A. intexta*, from the Lower Devonian (Lochkovian) of Salair, south-west Siberia, as type species by original designation. Earlier (Bogoyavlenskaya 1970) she attempted to introduce the genus without fixation of type species, a procedure not satisfying the criteria of availability of the International Code of Zoological Nomenclature (Article 13 (b); Ride et al. 1985). In another paper, Bogoyavlenskaya (1971) proposed a different generic name, *Columnoporella*, also with *A. intexta* as type

Fig. 29. Columnostroma clathratum sp. nov., × 10, Lilydale Limestone, Mitchell's (Cave Hill) Quarry, Lilydale; A, holotype NMV P141990 (*ex* NMV P13784), tangential section; B, paratype A NMV P141933 (*ex* NMV P13791), vertical section; C, paratype A NMV P141933 (*ex* NMV P13791), vertical section; D, paratype B NMV P141876, tangential section; E, paratype B NMV P141875, vertical section; F, paratype C NMV P37638, vertical section.
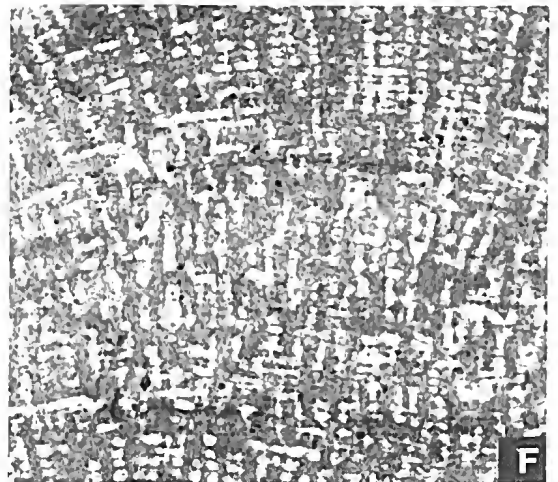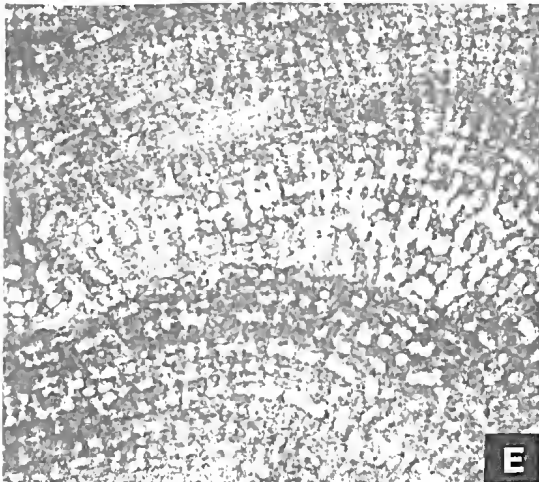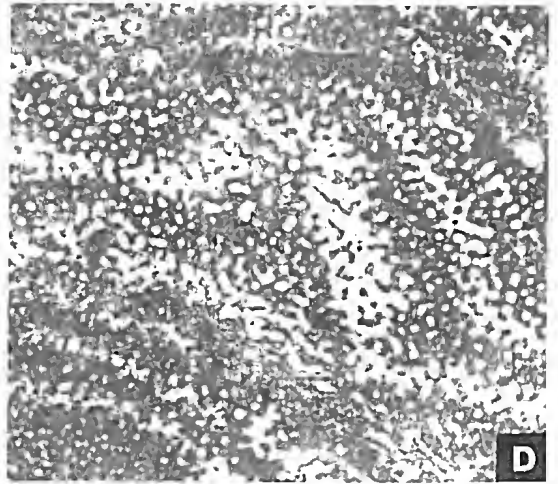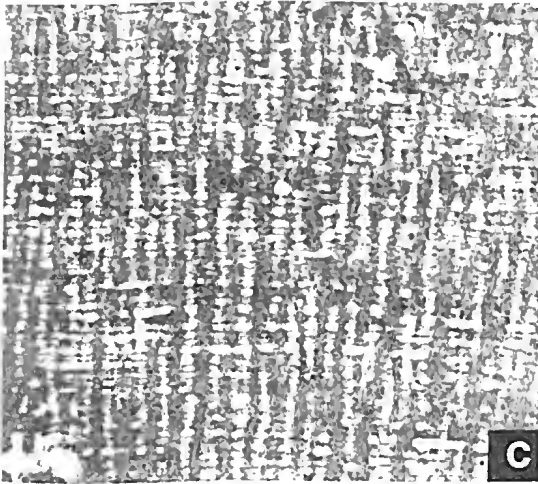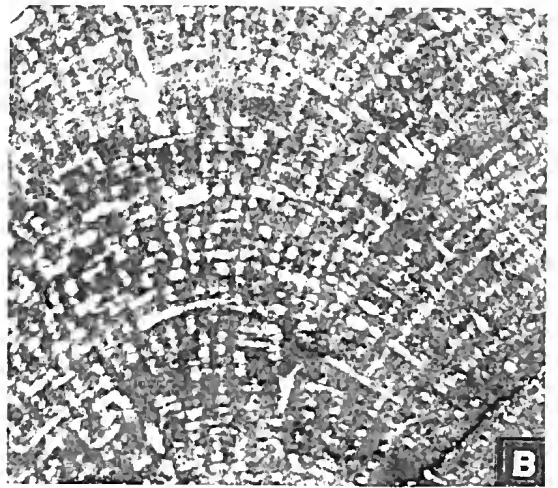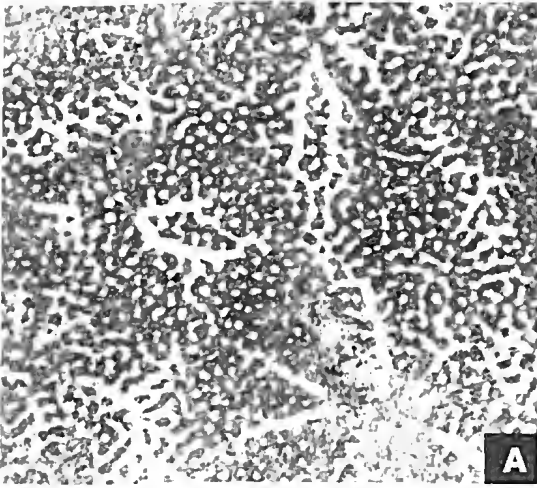
species, but this name is a junior homonym of *Columnoporella* Sokolov & Tesakov, 1963, a syringophyllid coral. The name *Columnoporella* is crossed out and *Stellopora* is substituted in handwriting in printed copies of Bogoyavlenskaya's 1971 paper, but this handwritten name is not validly published within the meaning of Article 9(1) of the Code. Consequently the name *Stellopora* dates from Bogoyavlenskaya's 1972 paper and not from the earlier publication of 1971 (cf. Bogoyavlenskaya 1973, Khromych 1974, Stearn 1980, Bogoyavlenskaya & Khromych 1985).

Dong & Wang (1982) introduced the genus *Columdictyon* (with type species *C. regulare* from the upper Middle Devonian of Yunnan, south China) to accommodate forms with upwardly and outwardly radiating pillars and associated upwardly arched laminae like *Stellopora*, but differing in lacking a clearly defined axial canal and marginal vesicles. It may be a matter of interpretation but Dong & Wang's (1982) figured type specimens do seem to show a few marginal vesicles and a very fine axial canal, so the justification for the separate genus is questioned. *Tianshanostroma*, based on *T. xinjiangense* Dong & Wang, 1984 from the Middle Devonian of Xinjiang, north-west China, has very similar upwardly and outwardly radiating pillars, upwardly arching laminae, an axial canal is apparently absent, and peripheral vesicles are not clearly developed. Consequently it is closely related to material previously referred to *Columdictyon* and should be tentatively included in *Stellopora*. A third, closely-related Chinese taxon is the basis for another doubtfully independent genus. In the description of *Qinghaipora* (type species *Q. gracilenta*, based on very poorly preserved specimens from the upper Middle to lower Upper Devonian of southern Qinghai), Dong (1991) emphasised skeletal elements dominated by long, closely spaced pillars, vague laminar elements and an axial canal. This material seems also to represent a species of *Stellopora*.

The dendroid and columnar genus *Stellopora* ranges from the Upper Silurian to the Upper Devonian but is most commonly found in Middle Devonian successions, given that 13 of

the 21 described species come from this interval. The genus is readily distinguished from *Amphipora* (based on type species *Caunopora ramosa* Phillips, 1841) by having long, radiating pillars extending outwards and upwards from near the axis. *Amphipora* has a similar growth habit and stratigraphic range, but has markedly different internal elements, notably axial and peripheral zones of amalgamate skeletal material without continuous pillars or laminae.

Stellopora porrecta sp. nov.

Fig. 30A–F

Amphipora ramosa.—Philip 1960: 153.—Philip 1962: 130.

Material. Numerous fragmentary stick-like branches have been cut from two rock samples (NMV P136389–91, *ex* NMV P136211; and NMV P136392–97, *ex* NMV P136212) from the Bell Point Limestone near the mouth of Bluff Creek, Waratah Bay. Holotype is NMV P136393, illustrated in longitudinal section in Fig. 30D. All other illustrated specimens are designated paratypes.

Derivation of name. Latin *porrectus*, alluding to the forwardly and outwardly directed pillars.

Diagnosis. A species of *Stellopora* with branches 1.7–3.5 mm in diameter, a small axial canal 0.25–0.6 mm (on average 0.3–0.4 mm) in diameter, two series of pillars 0.08–0.15 mm thick, and associated lateral processes, and a discontinuous row of marginal vesicles 0.3–0.5 mm wide.

Description. Skeleton consists of slender, stem-like branches up to 30 mm in length and from 1.7 to 3.5 mm (on average 2.6 mm) in diameter. Some branches show relatively unthickened internal structures, but in others much of the internal gallery space, except for areas of axial canals and marginal vesicles, is filled with thickened skeletal elements. The outer wall ranges from 0.06 to 0.1 mm in thickness, and the axial canal is from 0.25 to 0.5 mm (on average 0.3-0.4 mm) in width. Marginal vesicles are much larger than other gallery spaces, from 0.3 to 0.5 mm in width (measured radially from the outer wall inwards). Skeleton shows two series of pillars in cross section, with associated lateral

Fig. 30. Stellopora porrecta sp. nov., × 10, Bell Point Limestone, Bluff Creek, Waratah Bay; A, NMV P136395 (*ex* NMV P136212), transverse section; B, NMV P136392 (*ex* NMV P136212), vertical–oblique and transverse section; C, NMV P136396 (*ex* NMV P136212), oblique–vertical section; D, holotype NMV P136393 (*ex* NMV P136212), vertical section; E, NMV P136393 (*ex* NMV P136212), vertical section; F, NMV P136391 (*ex* NMV P136211), transverse section.
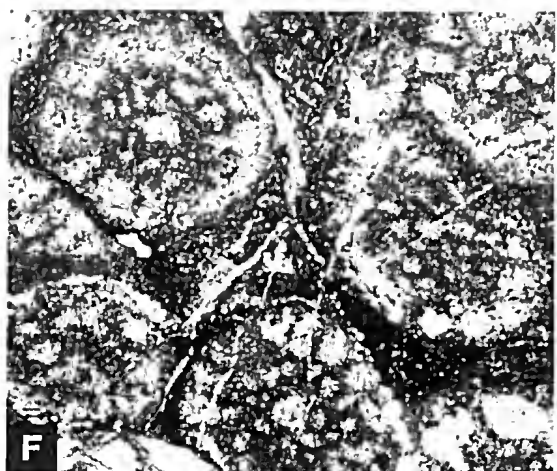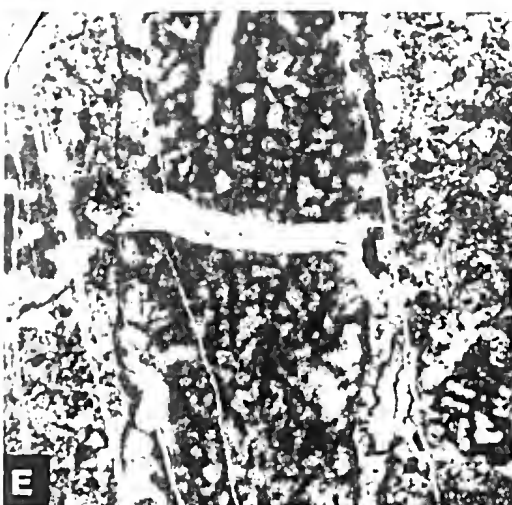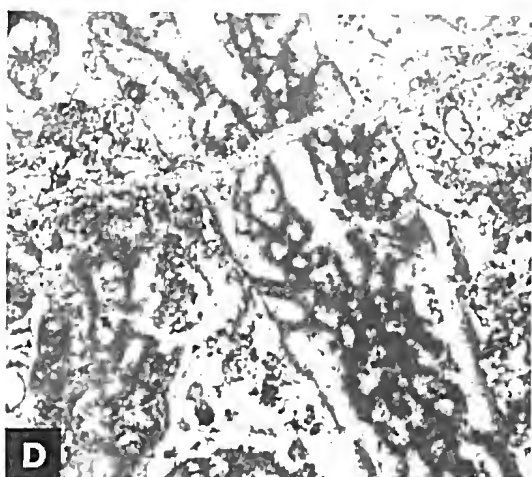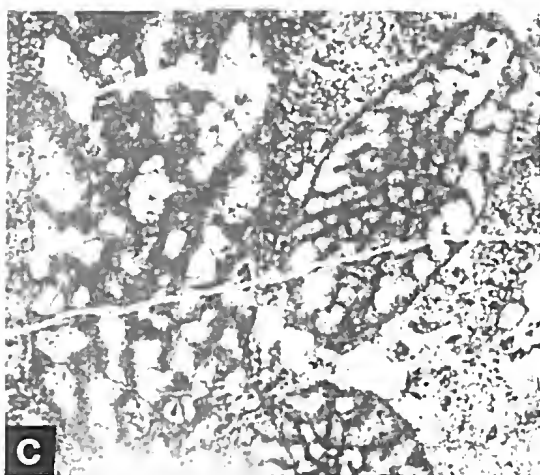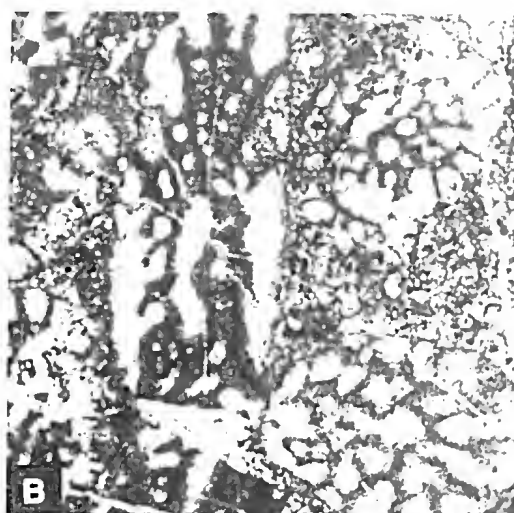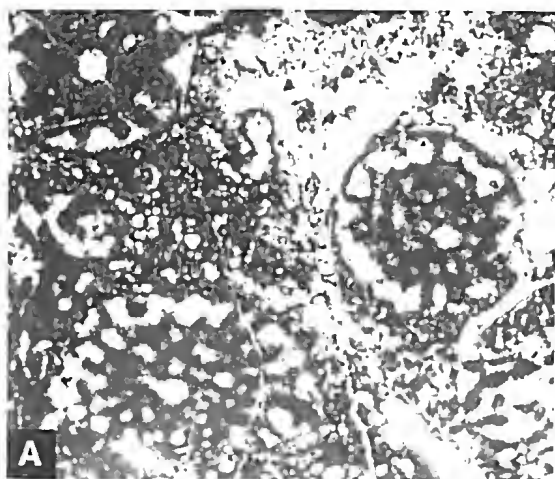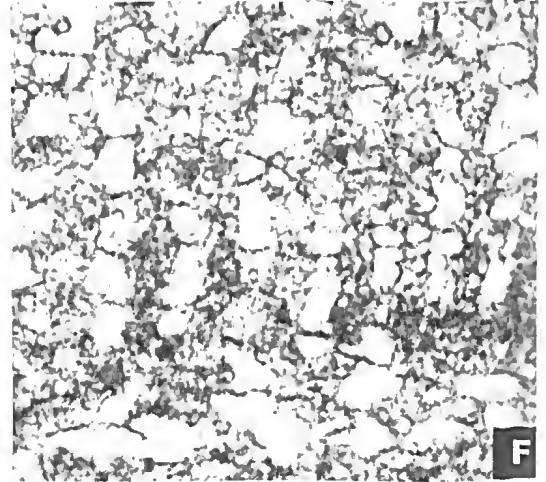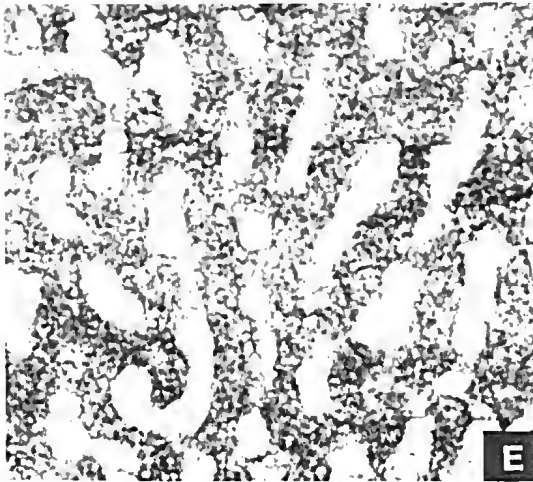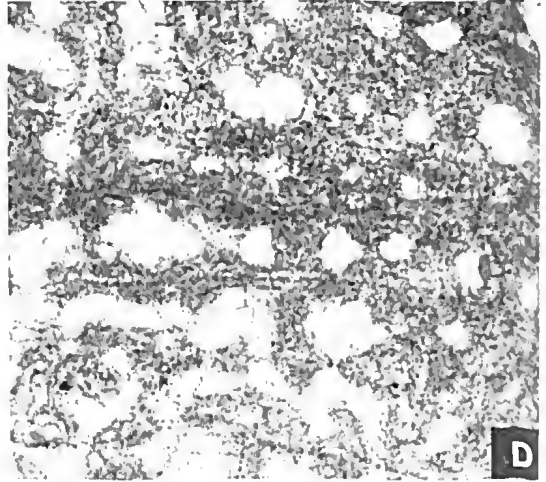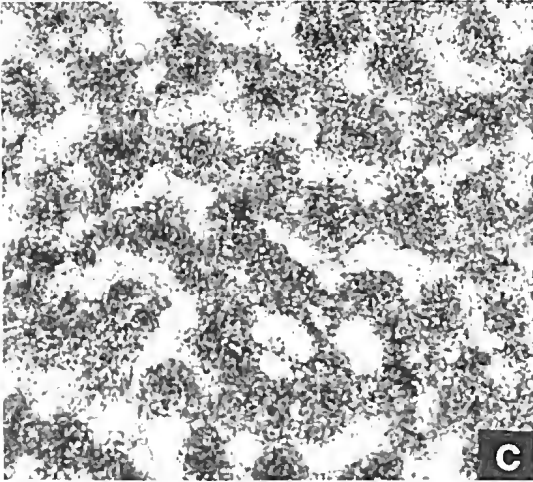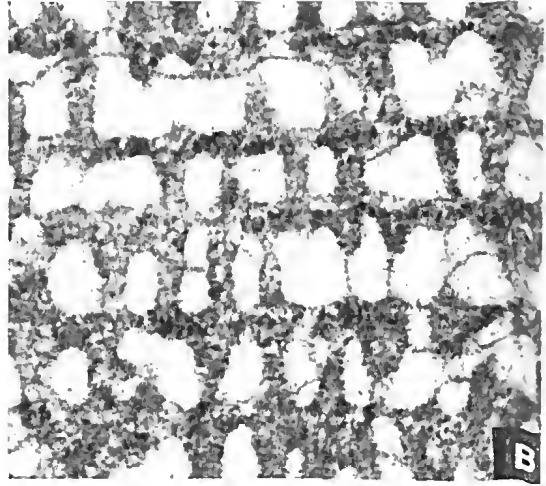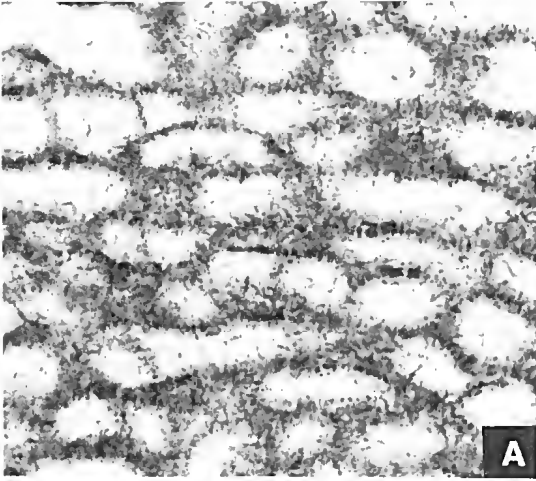
processes; pillars range markedly in thickness, from 0.08 to 0.15 mm, and show a median dark line (0.03 mm wide) between lighter layers with a fibrous microstructure at right angles to the dark line Dissepiments rare in axial canal and gallery spaces.

Remarks. 'Amphipora ramosa' has previously been recorded as occurring in the Bell Point Limestone, Waratah Bay (Philip 1960), and from the Coopers Creek Limestone at Tyers (Philip 1962). 'Amphipora biostromes' have also been reported from the Murrindal Limestone of the Buchan area (Teichert & Talent 1958: 10), and a single specimen is known from equivalent strata at Bindi (Philip 1960). These are probably all representatives of *Stellopora* but the Buchan, Bindi and Tyers material requires further study to confirm this and to establish groupings down to species level.

Few described species of *Stellopora* are closely similar to this new species. Forms like the type species, *S. intexta* from the Lower Devonian (Lochkovian) of Salair and the Middle Devonian of the southern Urals, and *S. karmakensis* (Yavorsky, 1957), also from the Lochkovian of Salair and possibly the Middle Devonian of Xinjiang, north-west China (Dong & Wang 1984), bear resemblances, but they have very slightly larger axial canals (0.4 mm in diameter) and overall a slightly finer network of structural elements (pillars and intersecting lateral processes). *S. karmakensis* also lacks continuity of marginal vesicles along the length of the branch.

Two other species may be compared. Both *S. rudis* (Lecompte, 1952) and *S. desquamata* (Lecompte, 1952), the latter formerly a subspecies of *Amphipora ramosa* (see Flügel & Flügel-Kahler 1968: 348), are from the Givetian–Frasnian successions of Belgium. *S. rudis* is also recorded from Givetian–Frasnian units of the Canning Basin, Western Australia (Cockbain 1984), and possibly from the Moravian karst (Frasnian) of the Czech Republic (Zukalová 1971). *S. rudis* differs from the Victorian Bell Point species in having slightly larger branch dimensions (3.0–3.5 mm in diameter) and a larger axial canal (0.5–0.8 mm in diameter). *S. desquamata* shows similar differences, as well as a reduced and less persistent row of marginal vesicles. The Western Australian representatives of *S. rudis* described by Cockbain (1984) similarly have on average larger branch diameters (mean 3.22 mm), larger axial canal diameters (mean 0.70 mm), and overall a slightly coarser network of internal stuctural elements (pillars and lateral processes).

Significantly, *S. rudis* is most abundant in the platform interior or back reef environments of the Upper Devonian reef complexes in the Canning Basin (Cockbain 1984), and it is likely that similar dominant occurrences like those of *S. porrecta* in the Bell Point Limestone at Waratah Bay are also environmentally diagnostic of the back reef biofacies.

ACKNOWLEDGEMENTS

Fig. 31. A, *Petridiostroma clarum* (Počta, 1894), NMV P136257 (*ex* NMV P136157), vertical section showing transverse fibrosity, × 30, Murrindal Limestone, Rocky Camp Quarry. B, *Stictostroma* sp., NMV P136291 (*ex* NMV P136172), vertical section showing tripartite microstructure and porous to transversely fibrous overprinting, × 30, Murrindal Limestone, Rocky Camp Quarry. C, D, *Amnestostroma holmesae* sp. nov., × 30, Lilydale Limestone, Mitchell's (Cave Hill) Quarry, Lilydale; C, paratype NMV P141976 (*ex* NMV P13776), tangential section showing pillars composed of finely cellular skeletal material; D, holotype NMV P141861 (*ex* MUGD 1619), vertical section showing tripartite laminae. E, *Salairella lilydalensis* (Ripper, 1937a), NMV P136311 (*ex* NMV P136216), vertical section showing fine cellular skeletal material, × 30, Coopers Creek Limestone, Tyers Quarry. F, *Parallelopora ampla* sp. nov., holotype NMV P136313 (*ex* NMV P136217), vertical section showing coarsely cellular skeletal material, × 30, Murrindal Limestone, Rocky Camp Quarry.
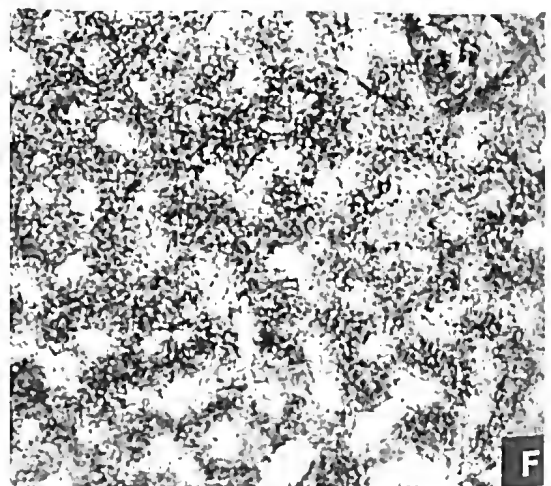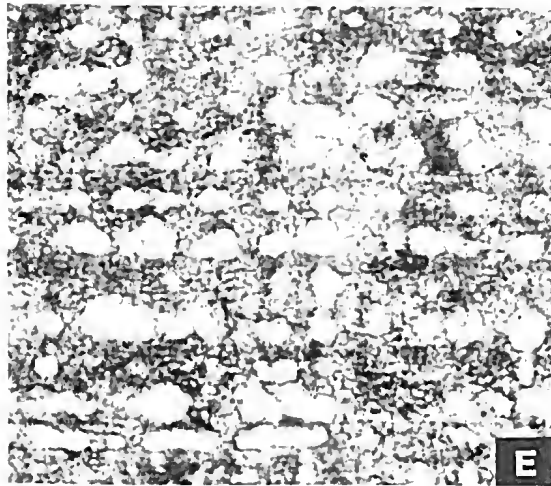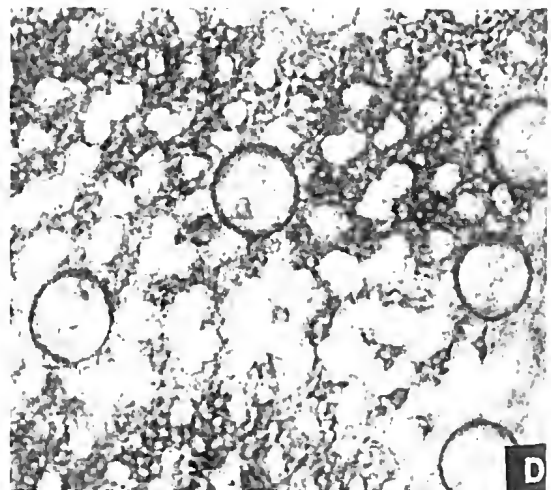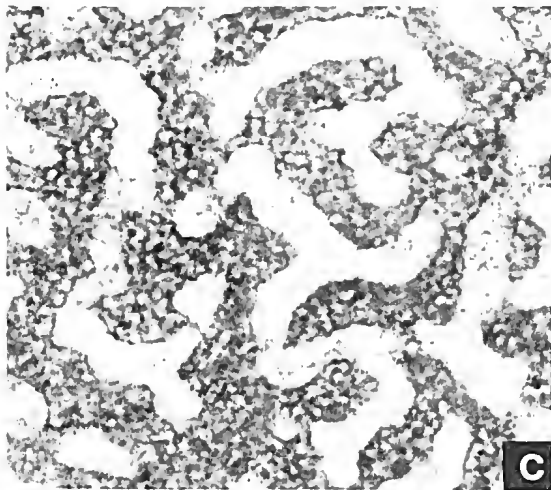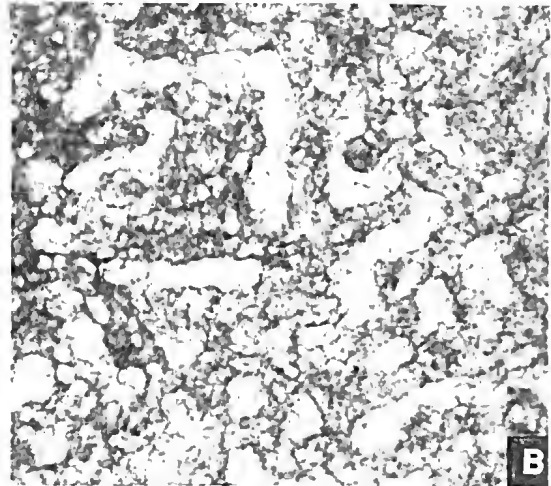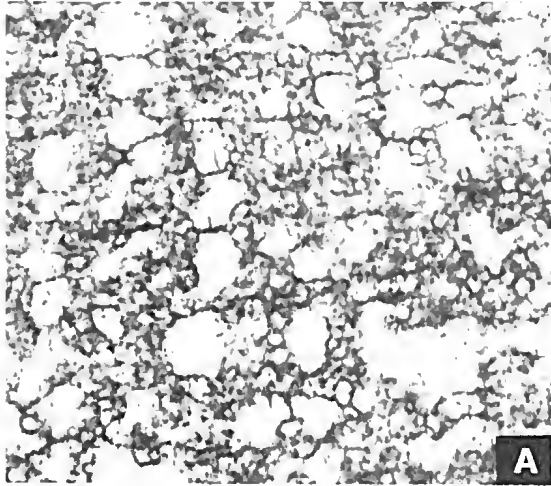
REFERENCES

BARGATZKY, A., 1881. Die Stromatoporen des rheinischen Devons. *Verhandlungen des Naturhistorischer Vereins der Preussischen Rheinlande, Westfalens und des Regierungsbezirks Osnabrück* 38: 233–304.

BIRKHEAD, P. K., 1967. Stromatoporoidea of Missouri. *Bulletins of American Paleontology* 52 (234): 23–110.

BIRKHEAD, P. K., 1986. Stromatoporoid biozonation of the Cedar City Formation, Middle Devonian of Missouri. *Journal of Paleontology* 60: 268–272.

BOGOYAVLENSKAYA, O. V., 1965. O taksonomicheskom znachenii astroriz u stromatoporoidei. In *Tabulatomorfnye korally devona i carbona SSSR*, B. S. Sokolov & V. N. Dubatolov, eds, Nauka, Moscow, 105–112.

BOGOYAVLENSKAYA, O. V., 1969. K postrocniyu klassifikatsii stromatoporoidei. *Paleontologicheskii zhurnal* 1969 (4): 12–27.

BOGOYAVLENSKAYA, O. V., 1970. Novye vidy stromatoporoidei iz amfiporoviyh izvestnykov srednego devona vostochnogo sklona Urala (Ivdelskii, Severouralskii rayony). In *Materialy po paleontologii Urala*, Institut geologii i geokhimii, Uralskii filial, Akademiya nauk SSSR, Sverdlovsk, 69–79.

BOGOYAVLENSKAYA, O. V., 1971. K revizii semeiystva Idiostromatidae Nicholson. In *Rugozy i stromatoporoidei paleozoya SSSR*, A. B. Ivanovski, ed., Nauka, Moscow, 98–111.

BOGOYAVLENSKAYA, O. V., 1972a. Novye rody stromatoporoidei iz silura Tuvy. *Paleontologicheskii zhurnal* 1972 (2): 26–31.

BOGOYAVLENSKAYA, O. V., 1972b. Otryad Stromato-poroidea Nicholson. In *Kishechnopolostniye i brachiopody zhivetskich otlozheniiy vostochnogo sklona Urala*, A. N. Chodalevich, ed., Nedra, Moscow, 24–43, 187–189, 204–215.

BOGOYAVLENSKAYA, O. V., 1973. *Siluriiskie stromatoporoidei Urala.* Nauka, Moscow, 1–95.

BOGOYAVLENSKAYA, O. V., 1977. Nekotoriye stromatoporoidei iz rannedevonskikh otlozhenii vostchnogo sklona Urala. In *Novye materialy po paleontologii Urala*, G. N. Papulov & M. G. Breivel, eds, Institut geologii i geokhimii, Ural'skii nauchniy tsentr, Akademiya nauk SSSR, Sverdlovsk, 13–30.

BOGOYAVLENSKAYA, O. V. & KHROMYCH, V. G., 1985. *Ukazatel' rodov i vidov stromatoporat.* Nauka, Moscow, 1–104.

CHAPMAN, F., 1912a. Report of fossils. Silurian and Devonian fossils from the Mitta Mitta district, NE Victoria. *Records of the Geological Survey of Victoria* 3: 216.

CHAPMAN, F., 1912b. Report on fossils: Middle Devonian of the Buchan district. *Records of the Geological Survey of Victoria* 3: 218–222.

CHAPMAN, F., 1913. On the palaeontology of the Silurian of Victoria. *Report of the Australasian Association for the Advancement of Science (Melbourne)* 14: 207.

CHAPMAN, F., 1914. Newer Silurian fossils of eastern Victoria, Part 3. *Records of the Geological Survey of Victoria* 3: 311.

COCKBAIN, A. E., 1965. Note on Devonian stromatoporoids from Reefton. *New Zealand Journal of Geology and Geophysics* 8: 745–751.

COCKBAIN, A. E., 1984. Stromatoporoids from the Devonian reef complexes, Canning Basin, Western Australia. *Geological Survey of Western Australia Bulletin* 129: 1–108.

COCKBAIN, A. E., 1985. Devonian stromatoporoids from the Carnarvon Basin, Western Australia. *South Australia Department of Mines and Energy Special Publication* 5: 29–33.

COCKBAIN, A. E., 1989. Distribution of Frasnian and Famennian stromatoporoids. *Memoirs of the Association of Australasian Palaeontologists* 8: 339–345.

CONAGHAN, P. J., MOUNTJOY, E. W., EDGECOMBE, D. R., TALENT, J. A. & OWEN D. E., 1976. Nubrigyn algal reefs (Devonian), eastern Australia: allochthonous blocks and megabreccias. *Bulletin of the Geological Society of America* 87: 515–530.

Fig. 32. A, B, *Parallelopora ampla* sp. nov., holotype NMV P136313 (*ex* NMV P136217), vertical and tangential sections showing coarse cellular skeletal material, × 30, Murrindal Limestone, Rocky Camp Quarry. C, *Syringostromella* cf. *labyrinthea* Stearn, 1990, NMV P141784 (*ex* MUGD 1615), tangential section showing cellular microstructure, × 30, Buchan Caves Limestone, Heath's Quarry. D, E, *Habrostroma tyersense* sp. nov., × 30, Coopers Creek Limestone, Tyers Quarry; D, NMV P136361 (*ex* NMV P136193), tangential section; E, holotype NMV P136342 (*ex* NMV P136185), vertical section showing cellular (microreticulate) microstructure. F, *Columnostroma clathratum* sp. nov., paratype A NMV P141933 (*ex* NMV P13791), tangential section showing fine cellular skeletal material, × 30, Lilydale Limestone, Mitchell's (Cave Hill) Quarry, Lilydale.

COOPER, B. J., 1973. Lower Devonian conodonts from Loyola, Vietoria. *Proceedings of the Royal Society of Victoria* 86: 77–84.

CROHN, P. W., 1953. Lilydale limestone deposit. *Mining and Geological Journal of Victoria* 5 (1): 37–41.

DÖDERLEIN, L., 1892. Über *Petrostroma schulzei* n. gen. n. sp. der Kalkschwämme. *Verhandlungen der Deutschen Zoologischen Gesellschaft* 2: 143–145.

DONG, D. Y., 1991. Middle and Upper Devonian stromatoporoids from southern Qinghai and the paleoecological characters. In *Devonian to Triassic Stratigraphy and Palaeontology of Yushu Region, Qinghai Province*, vol. 2, Nanjing University Press, Nanjing, 65–82. [In Chinese with English summary.]

DONG, D. Y. & WANG, B. Y., 1984. Paleozoic stromatoporoids from Xinjiang and their stratigraphic significance. *Bulletin of the Nanjing Institute of Geology and Palaeontology, Academia Sinica* 7: 237–286.

DONG, D. Y. & WANG, C. Y., 1982. Devonian stromatoporoids of eastern Yunnan. *Bulletin of the Nanjing Institute of Geology and Palaeontology, Academia Sinica* 4: 1–40.

FAGERSTROM, J. A., 1961. The fauna of the Middle Devonian Formosa Reef Limestone of southwestern Ontario. *Journal of Paleontology* 35: 1–48.

FAGERSTROM, J. A., 1982. Stromatoporoids of the Detroit River Group and adjacent rocks (Devonian) in the vicinity of the Michigan Basin. *Geological Survey of Canada Bulletin* 339: 1–81.

FLÜGEL, E., 1958a. Eine mitteldevonische Korallen-Stromatoporen-Fauna vom Plöcken-Pass (Kleiner Pal-Westflanke, Karnische Alpen). *Carinthia II* 68: 49–61.

FLÜGEL, E., 1958b. Die paläozoischen Stromatoporen-Faunen der Ostalpen, Verbreitung und Stratigraphie. *Jahrbuch der Geologischen Bundesanstalt* 101: 167–186.

FLÜGEL, E., 1958c. *Pseudoactinodictyon* n. gen. und *Actinodictyon* Parks (Stromatoporoidea). *Senckenbergiana lethaea* 39: 135–151.

FLÜGEL, E., 1959. Die Gattung *Actinostroma* Nicholson und ihre Arten (Stromatoporoidea). *Annalen des Naturhistorischen Museums in Wien* 63: 90–273.

FLÜGEL, E. & FLÜGEL-KAHLER, E., 1968. Stromatoporoidea (Hydrozoa palaeozoica). *Fossilium Catalogus, I: Animalia* 115: 1–416 (part 1); 116: 417–681 (part 2).

FRITZ, M. A. & WAINES, R. H., 1956. Stromatoporoids from the Upper Abitibi River Limestone. *Proceedings of the Geological Asssociation of Canada* 8: 87–126.

GALLOWAY, J. J. & ST JEAN, J., 1957. Middle Devonian Stromatoporoidea of Indiana, Kentucky, and Ohio. *Bulletins of American Paleontology* 37 (162): 25–308.

GARRATT, M. J., 1983. Silurian and Devonian biostratigraphy of the Melbourne Trough, Victoria. *Proceedings of the Royal Society of Victoria* 95: 77–98.

GARRATT, M. J. & WRIGHT, A. J., 1988. Late Silurian to Early Devonian biostratigraphy of southeastern Australia. *Canadian Society of Petroleum Geologists Memoir* 14 (3): 647–662.

GILL, E. D., 1940. The Silurian rocks of Melbourne and Lilydale: discussion of the Melbournian-Yeringian boundary and associated problems. *Proceedings of the Royal Society of Victoria* 52: 249–261.

GILL, E. D., 1942. On the thickness and age of the type Yeringian strata, Lilydale, Victoria. *Proceedings of the Royal Society of Victoria* 54: 21–53.

GIRTY, G. H., 1895. A revision of the sponges and coelenterates of the Lower Helderberg Group of New York. *State of New York, Annual Report of the State Geologist* 14: 259–309.

GLEN, R. A., SCHEIBNER, E., VANDENBERG, A. H. M., 1992. Paleozoic intraplate escape tectonics in Gondwanaland and major strike-slip duplication in the Lachlan orogen of southeastern Australia. *Geology* 20: 795–798.

GOLDFUSS, G. A., 1826. *Petrefacta Germaniae. I. Zoophytorum Reliquiae*. Arnz & Co., Düsseldorf, 252 p.

GORSKY, I. I., 1935. Nekotorye Coelenterata iz nizhnekamennougol'nykh otlozhenii Novoi Zemli. *Trudy Arkticheskogo nauchno-issledovatel'skogo instituta* 28: 2–128.

GREGORY, J. W., 1903. The Heathcotian—a pre-Ordovician series—and its distribution in Victoria. *Proceedings of the Royal Society of Victoria* 15: 148–175.

HILL, D., 1939. The Devonian rugose corals of Lilydale and Loyola, Victoria. *Proceedings of the Royal Society of Victoria* 51: 219–256.

IVANIYA, V. A. & KOSAREVA, E. G., 1968. K voprosu o vozraste Kur'inskikh izvestnyakov (severnoi chasti Rudnogo Altaya). *Trudy gosudarstvennogo Tomskogo universiteta, seriya geologicheskaya* 202: 67–82.

KHALFINA, V. K., 1961. Stromatoporoidea, Devonskaya sistema. In Biostratigrafiya paleozoya Sayano–Altaiskoi gornoi oblasti, Tom 2, Srednii paleozoi. *Trudy Sibirskogo nauchno-issledovatel'skogo instituta geologii, geofiziki i mineral'nogo syr'ya* 20: 245–256, 323–349.

KHALFINA, V. K., 1968a. O novykh rodakh stromatoporoidei iz devonskikh otlozhenii yuznoi okrainy Kuzbassa i Altaya. *Trudy gosudarstvennogo Tomskogo universiteta, scriya geologicheskaya* 202: 147–152.

KHALFINA, V. K., 1968b. Obzor kompleksov stromatoporoidei nizhnego i srednego devona Salaira. In *Materialy po regional'noi geologii Sibiri (Soveshchanie po stratigrafii devona Sibiri, Novosibirsk, 1967g.)*, L. L. Khalfin, ed., Sibirskii nauchno-issledovatel'skii institut geologii, geofiziki i mineral'nogo syr'ya (Seriya regional'naya geologiya), Novosibirsk, 57–69.

KHALFINA, V. K. & YAVORSKY, V. I., 1971. Novaya gruppa stromatoporoidei. *Trudy Instituta geologii i geofiziki Sibirskogo otdelenia Akademii nauk SSSR* 8: 118–121.

KHROMYCH, V. G., 1971. O stromatoporoideyakh nelyudimskoi svity (Severo-Vostok SSSR). In *Rugozy i stromatoporoidei paleozoya SSSR*, A. B. Ivanovski, ed., Nauka, Moscow, 125–134.

KHROMYCH, V. G., 1974. *Devonskie stromatoporoidei Severo-Vostoka SSSR*. Nauka, Sibirskoe otdelenie, Novosibirsk, 1–104.

KÜHN, O., 1927. Zur Systematik und Nomenklatur der Stromatoporen. *Zentralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B* 1927: 546–551.

LAUBENFELS, M. W. DE, 1955. Porifera. In *Treatise on Invertebrate Paleontology*, Part E, R. C. Moore, ed., Geological Society of America and University of Kansas Press, Lawrence, E21–E122.

LECOMPTE, M., 1951. Les Stromatoporoides du Dévonien moyen et supérieur du Bassin de Dinant. Première Partie. *Institut Royal des Sciences Naturelles de Belgique, Mémoires* 116: 1–215.

LECOMPTE, M., 1952. Les Stromatoporoides du Dévonien moyen et supérieur du Bassin de Dinant. Deuxième Partie. *Institut Royal des Sciences Naturelles de Belgique, Mémoires* 117: 216–359.

LE MAÎTRE, D., 1934. Études sur la faune des Calcaires Dévoniens du Bassin d'Ancenies, Calcaire de Chaudefonds et Calcaire de Chalonnes (Maine-et-Loire). *Mémoires de la Société Géologique du Nord* 12: 1–267.

LESOVAYA, A. I., 1970. Stromatoporoidei devona Zeravshanskogo khrebta. In *Biostratigrafiya osadochnykh obrazovanii Uzbekistana*, T. S. Shayakubov, ed., Nedra, Leningrad, 74–98.

LESOVAYA, A. I., 1972. Novye siluriiskie i nizhnedevonskie stromatoporoidei Yuzhnogo Tian-Shanya. In *Novye danniye po faune paleozoya i mesozoya Uzbekistana*, A. S. Masumov & R. N. Abdullaev, eds, Akademiya Nauk Uzbekskoy SSR, Fan, Tashkent, 46–52.

LESOVAYA, A. I., 1982. Ranne- i srednedevonskie stromatoporaty Yuzhnogo Tian-Shanya. In *Biostratigrafiya pogranichnykh otlozheniiy nizhnego i srednego devona*, B. S. Sokolov & M. A. Rzhonsnitskaya, eds, Nauka, Leningrad, 102–104.

LESOVAYA, A. I., 1986. Novye nizhnedevonskie stromatoporaty Zeravshanskogo khrebta. *Paleontologischeskii zhurnal* 1986 (1): 33–37.

LESOVAYA, A. I. & ZAKHAROVA, V. M., 1970. Novye stromatoporoidei iz verkhnego silura Turkestanskogo khrebta. *Paleontologischeskii zhurnal* 1970 (2): 47–51.

MALLETT, C. W., 1970a. Devonian stromatoporoids from the Broken River Formation, north Queensland. *Journal and Proceedings of the Royal Society of New South Wales* 103: 35–42.

MALLETT, C. W., 1970b. The stromatoporoid genera *Tienodictyon* and *Anostylostroma* in the Lower and Middle Devonian of north Queensland. *Proceedings of the Royal Society of Queensland* 81: 85–92.

MALLETT, C. W., 1971.The stromatoporoid genera *Actinostroma* Nicholson and *Nexililamina* gen. nov. from the Devonian Broken River Formation, north Queensland. *Proceedings of the Royal Society of Victoria* 84: 235–244.

MATTHEWS, S. C., 1973. Notes on open nomenclature and on synonymy lists. *Palaeontology* 16: 713–719.

MAWSON, R., 1987. Early Devonian conodont faunas from Buchan and Bindi, Victoria, Australia. *Palaeontology* 30: 251–297.

MAWSON, R. & TALENT, J. A., in press. Age of an Early Devonian carbonate fan and isolated limestone clasts and megaclasts, east-central Victoria. *Proceedings of the Royal Society of Victoria* 106.

MAWSON, R., TALENT, J. A., BEAR, V. C., BENSON, D. S. BROCK, G. A., FARRELL, J. R., HYLAND, K. A., PYEMONT, B. D., SLOAN, T. R., SORRENTINO, L., STEWART, M. I., TROTTER, J. A., WILSON, G. A. & SIMPSON, A. G., 1988. Conodont data in relation to resolution of stage and zonal boundaries for the Devonian of Australia. *Canadian Society of Petroleum Geologists Memoir* 14 (3): 485–527.

MAWSON, R., TALENT, J. A., BROCK, G. A. & ENGELBRETSEN, M. J., 1992. Conodont data in relation to sequences about the Pragian-Emsian boundary (Early Devonian) in southeastern Australia. *Proceedings of the Royal Society of Victoria* 104: 23–56.

MISTIAEN, B., 1985. Phénomènes récifaux dans le Dévonien d'Afganistan (Montagnes Centrales): analyse et systématique des stromatopores, volume 2. *Publications de la Société géologique du Nord* 11: 1–245.

MORI, K., 1968. Stromatoporoids from the Silurian of Gotland. Part 1. *Stockholm Contributions in Geology* 19: 1–100.

NESTOR, H. A., 1964. *Stromatoporoidei ordovika i llandoveri Estonii*. Akademiya nauk Estonskoi SSR, Institut geologii, Tallinn, 1–112.

NESTOR, H. A., 1966. *Stromatoporoidei venlocka i ludlova Estonii*. Akademiya nauk Estonskoi SSR, Institut geologii, Tallinn, 1–87.

NICHOLSON, H. A., 1873. On some new species of *Stromatopora. Annals and Magazine of Natural History*, Series 4, 12: 89–95.

NICHOLSON, H. A., 1875. Amorphozoa from the Silurian and Devonian formations. *Geological Survey of Ohio* 2 (2): 245–256.

NICHOLSON, H. A., 1886a. On some new or imperfectly-known species of stromatoporoids. *Annals and Magazine of Natural History*, Series

NICHOLSON, H. A., 1886b. A monograph of the British stromatoporoids. Part 1. *Monograph of the Palaeontographical Society, London* 39: 1–130.

NICHOLSON, H. A., 1889. A monograph of the British stromatoporoids. Part 2. *Monograph of the Palaeontographical Society, London* 42: 131–158.

NICHOLSON, H. A., 1891. A monograph of the British stromatoporoids. Part 3. *Monograph of the Palaeontographical Society, London* 44: 159–202.

NICHOLSON, H. A., 1892. A monograph of the British stromatoporoids. Part 4. *Monograph of the Palaeontographical Society, London* 46: 203–234.

NICHOLSON, H. A. & MURIE, J., 1879. On the minute structure of *Stromatopora* and its allies. *Journal of the Linnean Society of London, Zoology* 14: 187–246.

OEKENTORP, K., 1969. Kommensalismus bei Favositiden. *Münsterische Forschungen zur Geologie und Paläontologie* 12: 165–217.

OLIVER, W. A. & CHLUPÁČ I., 1991. Defining the Devonian: 1979–89. *Lethaia* 24: 119–122.

PARKS, W. A., 1936. Devonian stromatoporoids of North America, Part 1. *University of Toronto Studies, Geological Series* 39: 1–125.

PHILIP, G. M., 1960. Victorian Siluro-Devonian faunas and correlations. *International Geological Congress, Copenhagen* 21 (7): 143–157.

PHILIP, G. M., 1962. The palaeontology and stratigraphy of the Siluro-Devonian sediments of the Tyers area, Gippsland, Victoria. *Proceedings of the Royal Society of Victoria* 75: 123–246.

PHILIP, G. M., 1965. Lower Devonian conodonts from the Tyers area, Gippsland, Victoria. *Proceedings of the Royal Society of Victoria* 78: 95–117.

PHILIP, G. M. & PEDDER, A., 1967. Stratigraphical correlation of the principal Devonian limestone sequences of eastern Australia. In *International Symposium on the Devonian System*, vol. 2, D. H. Oswald, ed., Alberta Society of Petroleum Geologists, Calgary, 1025–1041.

PHILLIPS, J., 1841. *Figures and Descriptions of the Palaeozoic Fossils of Cornwall, Devon and West Somerset.* Longman, Brown, Green & Longmans, London, 231 p.

POČTA, P., 1894. *Systême Silurien du Centre de la Bohême par Joachim Barrande, 1ère Partie: Recherches Paléontologiques*, vol. 8 , part 1, *Bryozoaries, Hydrozoaries et partie des Anthozoaries.* Prague, 230 p.

RIDE, W. D. L., SABROSKY, C. W., BERNARDI, G. & MELVILLE, R. V. (eds), 1985. *International Code of Zoological Nomenclature*, 3rd edn. International Trust for Zoological Nomenclature and British Museum (Natural History), London, 338 p.

RIPPER, E. A., 1933. The stromatoporoids of the Lilydale Limestone. Part 1, *Actinostroma* and *Clathrodictyon. Proceedings of the Royal Society of Victoria* 45: 152–164.

RIPPER, E. A., 1937a. The stromatoporoids of the Lily-

dale Limestone. Part 2, *Syringostroma, Stromatopora*, and other genera. *Proceedings of the Royal Society of Victoria* 49: 178–205.

RIPPER, E. A., 1937b. On some stromatoporoids from Griffith's Quarry, Loyola, Victoria. *Proceedings of the Royal Society of Victoria* 50: 1–9.

RIPPER, E. A., 1937c. On the stromatoporoids of the Buchan district, Victoria. *Proceedings of the Royal Society of Victoria* 50: 11–45.

RIPPER, E. A., 1938. Notes on the Middle Palaeozoic stromatoporoid faunas of Victoria. *Proceedings of the Royal Society of Victoria* 50: 221–243.

ROSEN, F. B., 1867. Über die Natur der Stromatoporen und über die Erhaltung der Hornfasern der Spongien im fossilen Zustande. *Verhandlungen der Russisch-kaiserlichen mineralogischen Gesellschaft zu St-Petersburg*, Series 2, 4: 1–98.

RUKHIN, L. B., 1938. Nizhnepaleozoiskie korally i stromatoporoidei verkhnei ehasti basseina r. Kolymy. *Materialy po izucheniyu Kolymsko-Indigirskogo kraya*, Series 2, *Geologiya i Geomorfologiya* 10: 1–119.

SLEUMER, B. H. G., 1969. Devonian stromatoporoids of the Cantabrian Mountains (Spain). *Leidse Geologische Mededelingen* 44: 1–136.

SOKOLOV, B. S. & TESAKOV, Y. I., 1963. *Tabulyaty paleozoiya Sibiri.* Institut geologii i geofiziki, Sibiriskoe otdelenie, Akademiya nauk SSSR, Moscow & Leningrad, 188 p.

SPENCER, J. W., 1884. Niagaran Fossils. 2. Stromatoporoidea of the Upper Silurian System. *Bulletin of the Museum of the University of the State of Missouri* 1: 43–52.

STEARN, C. W., 1961. Devonian stromatoporoids from the Canadian Rocky Mountains. *Journal of Paleontology* 35: 932–948.

STEARN, C. W., 1966. The microstructure of stromatoporoids. *Palaeontology* 9: 74–124.

STEARN, C. W., 1979. Biostratigraphy of Devonian stromatoporoids. *Special Papers in Palaeontology* 23: 229–232.

STEARN, C. W., 1980. Classification of the Paleozoic stromatoporoids. *Journal of Paleontology* 54: 881–902.

STEARN, C. W., 1983. Stromatoporoids from the Blue Fiord Formation (Lower Devonian) of Ellesmere Island, Arctic Canada. *Journal of Paleontology* 57: 539–559.

STEARN, C. W., 1990. Stromatoporoids from the allochthonous reef facies of the Stuart Bay Formation (Lower Devonian), Bathurst Island, Arctic Canada. *Journal of Paleontology* 64: 493–510.

STEARN, C. W., 1991. A revision of *Anostylostroma, Atelodictyon*, and related genera (Paleozoic Stromatoporoidea). *Journal of Paleontology* 65: 611–622.

STEARN, C. W., 1992. *Petridiostroma*, a new name for *Petrostroma* Stearn, 1991, not *Petrostroma* Döderlein, 1892. *Journal of Paleontology* 66:

531.

STEARN, C. W., 1993. Revision of the order Stromatoporida. *Palaeontology* 36: 201–229.

STEARN, C. W. & MEHOTRA, P. N., 1970. Lower and Middle Devonian stromatoporoids from northwestern Canada. *Geological Survey of Canada, Paper* 70-13: 1–43.

STECHOW, E., 1922. Zur Systematik der Hydrozoen, Stromatoporen, Siphonophoren, Anthozoen und Ctenophoren. *Archiv für Naturgeschichte,* A, 88 (3): 141–155.

STOCK, C. W., 1988. Lower Devonian (Gedinnian) Stromatoporoidea of New York: redescription of the type specimens of Girty (1895). *Journal of Paleontology* 62: 8–21.

STOCK, C. W., 1989. Microreticulate microstructure in the Stromatoporoidea. *Memoirs of the Association of Australasian Palaeontologists* 8: 149–155.

STOCK, C. W., 1991. Lower Devonian (Lochkovian) Stromatoporoidea from the Manlius Formation of New York. *Journal of Paleontology* 65: 897–911.

STOCK, C. W. & HOLMES, A. E., 1986. Upper Silurian/ Lower Devonian Stromatoporoidea from the Keyser Formation at Mustoe, Highland County, west-central Virginia. *Journal of Paleontology* 60: 555–580.

TALENT, J. A., 1965. The stratigraphic and diastrophic evolution of central and eastern Victoria in Middle Palaeozoic times. *Proceedings of the Royal Society of Victoria* 79: 179–195.

TALENT, J. A., 1969. Geology of East Gippsland. *Proceedings of the Royal Society of Victoria* 82: 37–60.

TALENT, J. A., 1988. Organic reef-building: episodes of extinction and symbiosis? *Senckenbergiana lethaea* 69: 315–368.

TALENT, J. A. & BANKS, M. R., 1967. Devonian of Victoria and Tasmania. In *International Symposium on the Devonian System,* vol. 2, D. H. Oswald, ed., Alberta Society of Petroleum Geologists, Calgary, 147–163.

TALENT, J. A., BERRY, W. B. N., BOUCOT, A. J., PACKHAM, G. H. & BISCHOFF, G. C. O., 1975. Correlation of the Silurian rocks of Australia, New Zealand, and New Guinea. *Geological Society of America, Special Paper* 150: 1–108.

TEICHERT, C. & TALENT, J. A., 1958. Geology of the Buchan area, East Gippsland. *Memoir of the Geological Survey of Victoria* 21: 1–56.

VANDENBERG, A. H. M., 1971. Explanatory notes on the Ringwood 1:63 360 geological map. *Geological Survey of Victoria Report* 1971/1: 1–35.

VANDENBERG, A. H. M., 1975. Definitions and descriptions of Middle Ordovician to Middle Devonian rock units of the Warburton district, central Victoria. *Geological Survey of Victoria Report* 1975/6: 1–47.

VANDENBERG, A. H. M., 1988. Silurian–Middle Devonian. In *Geology of Victoria,* 2nd edn, J. G. Douglas & J. A. Fergusson, eds, Victorian Division, Geological Society of Australia Inc., Melbourne, 103–146.

WANG, S. B., 1978. Order Stromatoporoidea. In *Palaeontological Atlas of Southwest China, Sichuan,* part 1, *Sinian to Devonian.* Geological Publishing House, Beijing, 9–36. [In Chinese.]

WEBBY, B. D. & ZHEN, Y. Y., 1993. Lower Devonian stromatoporoids from the Jesse Limestone of the Limekilns area, New South Wales. *Alcheringa* 17: 327–352.

WINCHELL, A., 1866. *The Grand Traverse Region: a Report on the Geological and Industrial Resources of the Counties of Antrim, Grand Traverse, Benzie, and Leelanaw in the Lower Peninsula of Michigan.* Dr Chase's Steam Printing, Ann Arbor, 97 p.

WINCHELL, A., 1867. Stromatoporoidae: their structure and zoological affinities. *Proceedings of the American Association for the Advancement of Science* 15: 91–99.

YANG, J. Z. & DONG, D. Y., 1979. Devonian stromatoporoids from central and eastern parts of Guangxi, China. *Palaeontologica sinica, new series B* 157 (14): 1–89.

YAVORSKY, V. I., 1929. Siluriiskie Stromatoporoidea. *Izvestiya geologicheskogo komiteta* 48: 77–114.

YAVORSKY, V. I., 1930. Actinostromidae iz devonskikh otlozhenii Urala i okrainy Kuznetskogo basseina. *Izvestiya geologicheskogo komiteta* 49: 473–496.

YAVORSKY, V. I., 1931. Nekotorye devonskie Stromatoporoidea iz okrain Kuznetskogo basseina, Urala i drugikh mest. *Izvestiya vsesoyuznogo geologo-razvedochnogo ob'edineniya* 50: 1387–1415.

YAVORSKY, V. I., 1955. Stromatoporoidea Sovetskogo Soyuza. Part I. *Trudy vsesoyuznogo nauchno-issledovatel'skogo geologicheskogo instituta, novaya seriya* 8: 1–173.

YAVORSKY, V. I., 1957. Stromatoporoidea Sovetskogo Soyuza. Part 2. *Trudy vsesoyuznogo nauchno-issledovatel'skogo geologicheskogo instituta, novaya seriya* 18: 1–165.

ZUKALOVÁ, V., 1971. Stromatoporoidea from the Middle and Upper Devonian of the Moravian Karst. *Rozpravy Ústředního ústavu geologického* 37: 1–143.

CORRIGENDUM

ARCHBOLD, N. W., 1993. Studies on Western Australian Permian brachiopods 11. New genera, specics and records. *Proceedings of the Royal Society of Victoria* 105: 1–29.

Due to a printing error the caption for Fig. 6 in this paper is incomplete. The complete caption is reproduced below.

Fig. 6. Svalbardia narelliensis Archbold. A, GSWA F43859, latex east of mature dorsal valve internal mould, × 3. B, GSWA F48360, latex east of dorsal valve internal mould, × 3. C, GWSA F43861, latex east of dorsal valve internal mould, × 3.5. D, GSWA F43862, latex east of juvenile dorsal valve internal mould, × 3.6. E, GSWA F43863, latex east of juvenile dorsal valve internal mould, × 3.5. F, GSWA F43864, latex east of juvenile ventral valve external mould, × 3.5. G, GSWA F43865, latex east of mature ventral valve internal mould, × 3.2. H, GSWA F43866, latex east of ventral valve external mould, × 3. I, GSWA F43867, latex east of ventral valve external mould, × 2.8. J, GSWA F43868, latex east of dorsal valve external mould, × 3.2.

AKTASTINIAN (EARLY ARTINSKIAN, EARLY PERMIAN) BRACHIOPODS FROM THE JIMBA JIMBA CALCARENITE, WOORAMEL GROUP, CARNARVON BASIN, WESTERN AUSTRALIA

N. W. Archbold and G. R. Shi

School of Aquatic Science and Natural Resources Management, Deakin University, Rusden Campus, 662 Blackburn Road, Clayton, Victoria 3168

Archbold, N. W. & Shi, G. R., 1993:11:01. Aktastinian (Early Artinskian, Early Permian) brachiopods from the Jimba Jimba Calcarenite, Wooramel Group, Carnarvon Basin, Western Australia. *Proceedings of the Royal Society of Victoria* 105 (2): 187–202. ISSN 0035-9211.

The brachiopod fauna of the Jimba Jimba Calcarenite, Carnarvon Basin, Western Australia is reviewed and described. New species named are *Neochonetes (Sommeriella) cockbaini*, *Cleiothyridina ovalis* and *Crassispirifer condoni*. The fauna is assigned to the *Strophalosia jimbaensis* Zone and an Aktastinian (Early Permian) age is preferred for the fauna.

THE CARNARVON Basin contains the best preserved Early Permian marine succession of all the Western Australian intracratonic basins and one of the richest sequences of Permian Gondwanan marine faunas. Brachiopod faunas from the Wooramel Group have received relatively minor attention until recently, apart from a few species from the Jimba Jimba Calcarenite described by Waterhouse (1970), Archbold (1983, 1986) and Archbold & Thomas (1986a), and small faunas from the One Gum and Billidee formations recently documented by Archbold (1991). The present study describes the moderately diverse brachiopod fauna of the Jimba Jimba Calcarenite which is stratigraphically below the Billidee Formation. This fauna has been referred to in several reports (Condon 1967, Thomas 1969, Playford et al. 1975) although only a few specimens have been described and figured. Documentation of the fauna confirms its biostratigraphical importance as well as its faunal relationship with, and distinction from, the fauna of the Callytharra Formation, which is stratigraphically below the Wooramel Group.

STRATIGRAPHY

The stratigraphy and structure of the Carnarvon Basin have been reviewed by Playford et al. (1975) and by Hocking et al. (1987). Only the pertinent stratigraphy concerning the Jimba Jimba Calcarenite is summarised below.

The Jimba Jimba Calcarenite was originally proposed by Condon (1965: 7) as a 'formation of fossiliferous calcarenite with calcilutite and sandstone conformably between the Moogooloo Sandstone below and the Billidee Formation above'. This calcarenite was also treated as a formational unit by Playford et al. (1975), but van de Graaff et al. (1977) and Hocking et al. (1987) considered the Jimba Jimba Calcarenite to be a member at the base of the Billidee Formation. We retain the unit as a formation because, although limited in outcrop, it is clearly mappable as shown by Condon (1967).

At its type section 15 km west of the Jimba Jimba Homestead the Jimba Jimba Calcarenite is 61 m thick. The unit is also recognised 14 km east of the type section (Condon 1967).

PREVIOUS FAUNAL STUDIES

No fossils were listed from the Jimba Jimba Calcarenite by Condon (1965) who considered its age to be Artinskian 'by reference to its position above the Callytharra Formation'. Later, Condon (1967: 88–91) provided a short list of fossil names and noted that the Jimba Jimba fauna was 'superficially very like that of the Callytharra Formation'. His list included Bryozoa, crinoid ossicles, *Linoproductus* spp., *Neospirifer* spp., *Cleiothyridina*, *Phricodothyris*, *Dictyoclostus*, *'Chonetes'* and *Derbyia*. Additional fossil collections from the Jimba Jimba Calcarenite were made by Dr A. E. Cockbain and Mr B. S. Ingram in 1966 from the Kennedy Range Dam site. Cockbain (1966) compared the fauna and lithology of the Jimba Jimba Calcarenite with those of the underlying Callytharra Formation and concluded that the gross faunal and lithological aspects of the two units were nearly identical. In the same report, Cockbain listed for both the Jimba Jimba Calcarenite and the Callytharra Formation the following taxa: *Neochonetes*

pratti (Davidson), *Dictyoclostus callytharrensis* (Prendergast), *Linoproductus cora foordi* (Etheridge) and *Neospirifer* spp. Waterhouse (1970) described and figured *Stepanoviella flexuosa* from the Jimba Jimba Calcarenite and also favoured an Aktastinian age for the unit.

Dickins (1963) drew attention to the molluscan faunas of the Wooramel Group, proposed a faunal Stage C for the bulk of the unit, and pointed out the close relationship of the assemblage with that of his Stage B (representing faunas from the Callytharra Formation and equivalent units). He indicated an Early Artinskian (Aktastinian) for Stage C. Runnegar (1969) and Waterhouse (1970) questioned the validity of Dickins's Stage C and suggested that it should be combined with Stage B. As a result, Cockbain (1980) considered the combined Stage B and C to be one biostratigraphical unit of 'a fairly long time range occurring at a number of shelly horizons, often of limited extent', and considered that it could not be used for detailed biostratigraphical correlation.

AGE OF THE JIMBA JIMBA CALCARENITE FAUNAL ASSEMBLAGE

The Aktastinian age usually ascribed to the Jimba Jimba Calcarenite was principally based on the stratigraphical position of the unit (overlying the Callytharra Formation and underlying the Billidee Formation) and the close relationship of the fauna with that of the Callytharra Formation. Ammonoids from the Callytharra Formation and the top of the Billidee Formation are regarded as indicating late Sakmarian (Sterlitamakian) and late Artinskian (Baigendzhinian) ages respectively (Glenister & Furnish 1961, Hocking et al. 1987). Alternative suggestions that the Wooramel Group may be Baigendzhinian in age (Cockbain 1980) have been discussed by Archbold (1991).

Dickins (1963) and Archbold (1991) concluded that, although the Wooramel Group and the Callytharra Formation have some species in common, the two faunas have distinctive elements. Further data to support this view are presented in the present study. Several brachiopod species from the Jimba Jimba Calcarenite occur in the Callytharra Formation, including *Callytharrella callytharrensis* (Prendergast), *Neospirifer* cf. *N. hardmani* (Foord), *Trigonotreta neoaustralis* Archbold & Thomas and *Cleiothyridina* cf. *C. baracoodensis* (Etheridge). Species occurring abundantly in, and confined

to, the Wooramel Group include *Strophalosia jimbaensis* Archbold (known from the Jimba Jimba Calcarenite and from both the One Gum and Billidee formations), *Neochonetes (Sommeriella) cockbaini* sp. nov., *Cleiothyridina ovalis* sp. nov. and *Globiella flexuosa* Waterhouse (all restricted to the Jimba Jimba Calcarenite). Characteristic species from the Callytharra Formation such as *Permorthotetes callytharrensis* Thomas, *Tornquistia occidentalis* Archbold, *Stictozoster senticosa* (Hosking), *Strophalosia irwinensis* Coleman, *Heteralosia etheridgei* (Prendergast), *Elivina hoskingae* Archbold & Thomas, *Tomiopsis woodwardi* Archbold & Thomas and *Spirelytha fredericksi* Archbold & Thomas have not been discovered in the Wooramel Group. There are also differences between the Callytharra Formation and the Wooramel Group in the bivalve and gastropod faunas (Dickins 1963: 10, also figs 3–5). Foraminifera from the Jimba Jimba Calcarenite are distinctive and represent a younger zone than those of the Callytharra Formation (Palmieri 1990).

In summary, in view of the distinctive and abundant species confined to the Wooramel Group and the many characteristic forms of the Callytharra Formation which are absent from the Wooramel Group, we consider that the fauna from the Wooramel Group represents an important and separable biostratigraphical horizon. An Aktastinian age was argued for the Wooramel Group by Archbold (1991).

PRESERVATION, DEPOSITORIES AND LOCALITIES

Material from the Jimba Jimba Calcarenite is moderately well preserved, generally as calcareous shells, but many specimens are incomplete and frequently decorticated because of the difficulty of extracting specimens from a limestone. Specimens occur in a relatively homogeneous, in some cases friable, grey to yellow fossiliferous calcarenite with minor calcilutite consisting predominantly of brachiopod, bryozoan and crinoid fragments.

The described material is housed in the Geological Survey of Western Australia, Perth (GSWA) and the Australian Geological Survey Organisation, Canberra (AGSO). GSWA material was collected by Dr A. E. Cockbain and Mr B. S. Ingram from a reference section of the Jimba Jimba Calcarenite at the Kennedy Range Dam site (GSWA field numbers F6243–F6248,

F6251–F6254) and by Dr S. K. Skwarko from the type section of the Jimba Jimba Calcarenite (GSWA field number 94218). The Kennedy Range Dam site is across the Gascoyne River, just north of the Jimba Jimba type locality. AGSO material was also collected from the type section of the Jimba Jimba Calcarenite (AGSO locality WO3) and is registered in the Commonwealth Palaeontological Collection (numbers with CPC prefix).

SYSTEMATIC PALAEONTOLOGY

The brachiopod fauna of the Jimba Jimba Calcarenite consists of the following species. All species are illustrated but only new species and material adding to the description of previously named species are described in this study.

Permorthotetes cf. *P. lindneri* Thomas, 1958 (Fig. 8A)
Neochonetes (Sommeriella) cockbaini Archbold sp. nov. (Fig. 1A–L)
Strophalosia jimbaensis Archbold, 1986 (Fig. 2A–J)
Reedoconcha? sp. (Fig. 3A)
Callytharrella callytharrensis (Prendergast, 1943) (Fig. 3N, O)
Costatumulus cf. *C. irwinensis* (Archbold, 1983) (Fig. 3C–G, L)
Globiella flexuosa (Waterhouse, 1970) (Fig. 3B, H–K)
Productidina or Chonetidina indet. (Fig. 3M)
Cleiothyridina ovalis Shi sp. nov. (Fig. 4A–P)
Cleiothyridina cf. *C. baracoodensis* (Etheridge, 1903) (Fig. 5A–G)
Cyrtella? sp. (Fig. 6A, B)
Neospirifer hardmani (Foord, 1890) (Fig. 6C–E, J)
Neospirifer cf. *N. foordi* Archbold & Thomas, 1986a (Fig. 6F–I, K)
Crassispirifer condoni Archbold & Shi sp. nov. (Fig. 7A–N)
Trigonotreta neoaustralis Archbold & Thomas, 1986a (Fig. 8B–E)
Tomiopsis cf. *T. rarus* Archbold & Thomas, 1986b (Fig. 8G–I)
Spirelytha sp. (Fig. 8F)
Hoskingia? sp. (Fig. 8J)

Order CHONETIDA Nalivkin, 1979
Suborder CHONETIDINA Muir-Wood, 1955
Superfamily CHONETACEA Bronn, 1862
Family RUGOSOCHONETIDAE Muir-Wood, 1962

Subfamily RUGOSOCHONETINAE Muir-Wood, 1962

Genus Neochonetes Muir-Wood, 1962
Subgenus Neochonetes (Sommeriella) Archbold, 1982

Type species. Chonetes prattii Davidson, 1859.

Neochonetes (Sommeriella) cockbaini Archbold sp. nov.

Fig. 1A–L

Neochonetes (Sommeria) pratti.—Archbold 1981: 114, fig. 5V, W (*non cet.*).

Etymology. For Dr A. E. Cockbain, geologist and palaeontologist.

Holotype. CPC 19869, a complete shell, from the type section of the Jimba Jimba Calcarenite (AGSO locality WO3).

Paratypes. GSWA F43871–F43872, two juvenile dorsal valves, from GSWA locality F6244; GSWA F43873, one mature dorsal valve, from GSWA locality F6252; CPC 31484-31488, CPC 19869, one incomplete dorsal valve, four complete shells and one incomplete shell, all from AGSO locality WO3.

Size ranges. Maximum width: 14–40 mm; hinge width: 14–36 mm; shell height: 8–24 mm; shell thickness: 5–9 mm.

Diagnosis. Very large *Neochonetes (Sommeriella)* with deep, relatively narrow sulcus and robust dorsal septa at maturity.

Description. Convexity of ventral valve distinct with prominent sulcus arising close to umbo, usually with deep median valley. Dorsal valve planar to gently concave with narrow, distinct fold developed anterior to umbo, broadening to anterior valve margin. Greatest width of shell at midlength or anterior to midlength. Exterior surface with weakly developed growth lines and fine capillae (about 3–4 per mm at 1 cm from umbo), increasing in number by bifurcation. Ventral interarea low, dorsal interarea very low. Cardinal spines poorly known. Ventral umbo low, rounded.

Ventral interior poorly known. Teeth short, stout. Delthyrium broad, relatively small.

Cardinal process low, robust at maturity. Chilidium not known. Alveolus deep, prominent at base of process at maturity. Socket ridges prominent, sockets distinct, deep, lateral septa and median septum prominent and thickened at maturity, weakly developed in submature individuals. Brachial ridges indistinct. Interior of submature valves with rows of radial papillae.
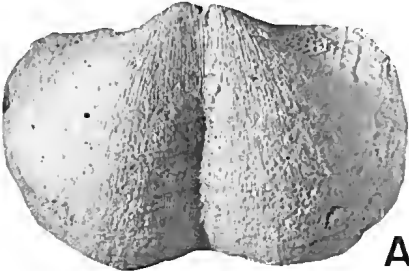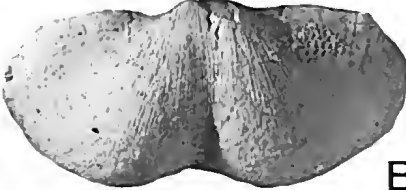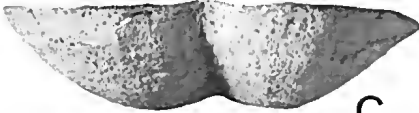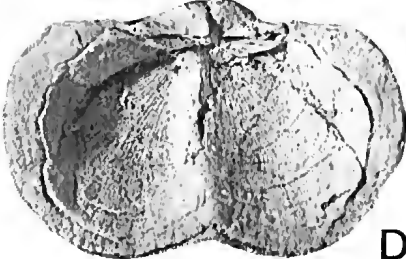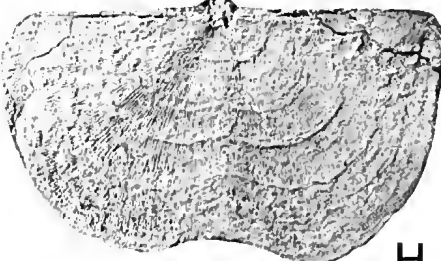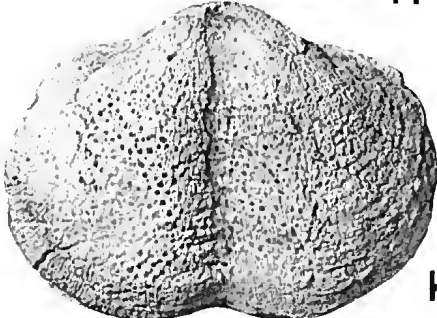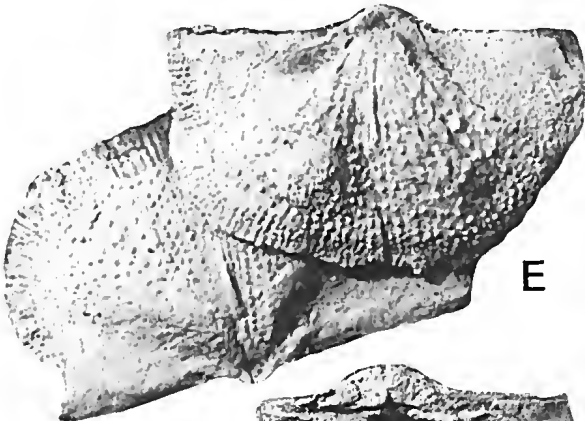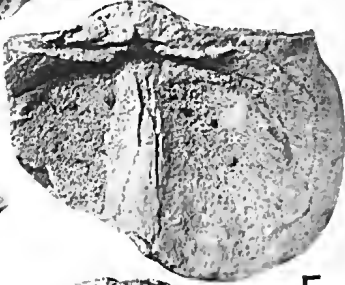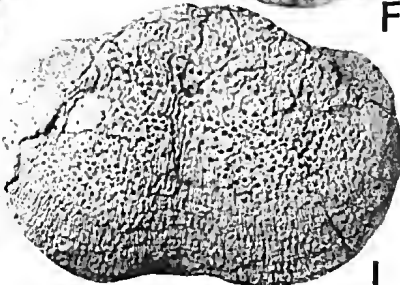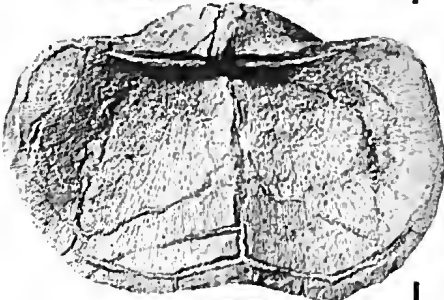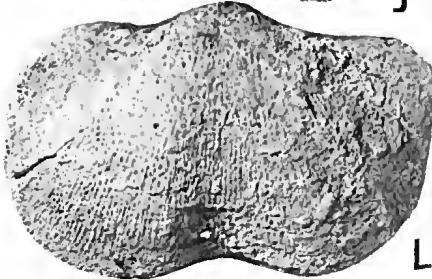
Fig. 1. Neochonetes (Sommeriella) cockbaini Archbold sp. nov. A–D, CPC 19869, holotype, complete shell in ventral, posteroventral, anterior and dorsal views, × 1.8. E, GSWA F43871–F43872, juvenile dorsal valves, interior views, × 3.5. F, CPC 31485, incomplete shell in dorsal view, × 1.8. G, CPC 31484, incomplete dorsal valve, interior view, × 2. H, GSWA F43873, dorsal valve exterior view, × 1.5. I–J, CPC 31486, shell in ventral and dorsal views, × 1.8. K, CPC 31487, shell in ventral view, × 2. L, CPC 31488, shell in ventral view, × 2.5.

At full maturity papillae restricted to anterior and lateral margins of valve interior. Posterior margin of valve smooth.

Discussion. This distinctive large species can be differentiated from *N. (S). prattii* (Davidson) (see Archbold 1981 for description of species) by its large size, characteristic deep sulcus and robust dorsal septa at maturity. *N. (S.) prattii* from the Sterlitamakian Callytharra Formation and correlative units in Western Australia is probably ancestral to *N. (S.) cockbaini.*

The younger species *N. (S.) tenuicapillatus* Archbold, 1981 from the Late Baigendzhinian Wandagee Formation possesses a more deeply concave dorsal valve and finer capillae than the new species.

Order PRODUCTIDA Sarycheva & Sokolskaya, 1959

Suborder STROPHALOSIIDINA Waterhouse, 1975

Superfamily STROPHALOSIACEA Schuchert, 1913

Family STROPHALOSIIDAE Schuchert, 1913

Subfamily STROPHALOSIINAE Schuchert, 1913

Genus Strophalosia King, 1844

Type species. Strophalosia gerardi King, 1846.

Strophalosia jimbaensis Archbold, 1986

Fig. 2A–J

Strophalosia jimbaensis Archbold 1986: 102, fig. 2A–G.—Archbold 1991: 60, fig. 3A–P (with synonymy).

Holotype. CPC 24405, a conjoined shell from the type section of Jimba Jimba Calcarenite, Carnarvon Basin, figured by Archbold (1986).

Size ranges. Maximum width: 26–43 mm; hinge width: 12–25 mm; shell height: 25–39 mm; shell thickness: ?5–18 mm; ventral interarea height: 1.5–4 mm; dorsal interarea height: 1–2 mm.

Description. Juvenile or submature shells slightly elongately oval in outline, mature specimens transversely oval; maximum width at midlength.

Hinge width varies from about 0.43 of maximum width to 0.70 of maximum width. Ventral interarea broadly triangular in shape in most specimens, rarely high and narrowly triangular, flat or very gently concave, finely striated parallel to hinge line. Delthyrium relatively small and narrow, filled with small, gently convex pseudodeltidium. Umbo small and broad, little extended, with broad umbonal angle varying from 93° to 130°, truncated by usually weakly developed cicatrix which is relatively small (4 mm in diameter in largest specimens). Ears very small, ill-defined. Cardinal extremities broadly rounded. Umbonal slopes gently convex. Lateral and anterior slopes high and steep. Gentle median sulcus is present in most ventral specimens examined, commences from about posterior third of shell curvature length and persists until anterior margin of shell, always shallow and broad, strongest over midlength of valve. Dorsal valve moderately and evenly concave. Dorsal interarea distinct, broad, usually slightly lower than ventral interarea, bisected by small, triangular notothyrium filled by gently convex chilidium.

Ventral valve ornament consists of spines and broad, weakly developed concentric lamellae. Coarse, suberect spines appear in a row along hinge line and in up to three rows on ears, 0.8 mm across spine base. Body spines numerous and evenly scattered on venter, slightly smaller than spines on ears, suberect, with swollen bases about 0.6–1 mm across, quincuncially arranged, 2–2.5 mm apart. Concentric lamellae ill-defined in most specimens; fine growth lamellae at times crowded together to form broad steps 2–5 mm wide. Dorsal valve lacks spines but possesses strongly developed concentric lamellae, 5–8 in 5 mm, and quincuncially arranged subcircular to elongate dimples which are 0.8–1 mm in diameter and numbering 3–4 in 5 mm.

Cardinal process arises from strong median septum and lateral ridges which surround small, deep sockets. Cardinal process moderately high, erect, inclined at up to 65° to plane of dorsal visceral disc, trilobed in external view with central lobe being most prominent, quadrilobed in internal view because of development of fine median depression on central lobe. Median septum extends to about midlength of dorsal valve, with tapering anterior end. Adductors
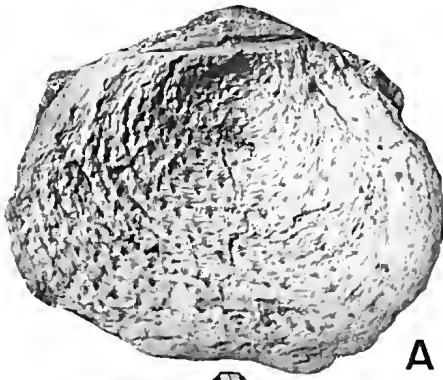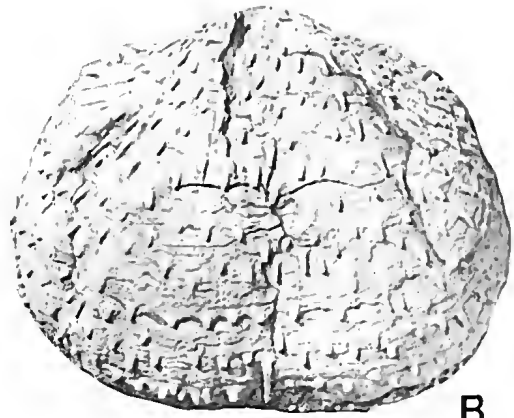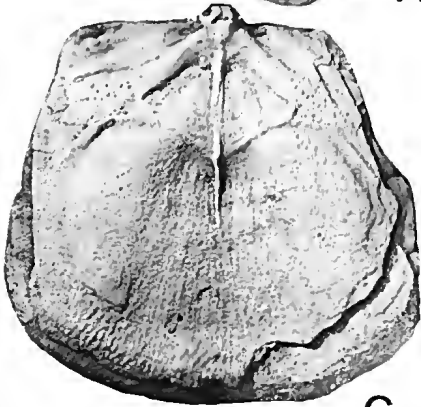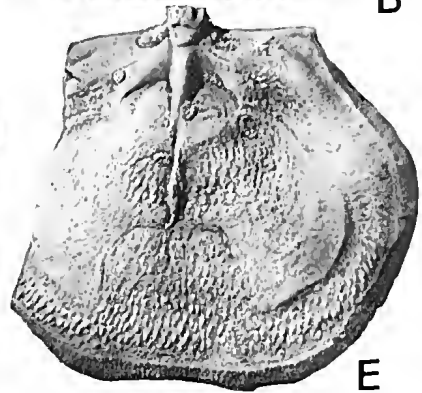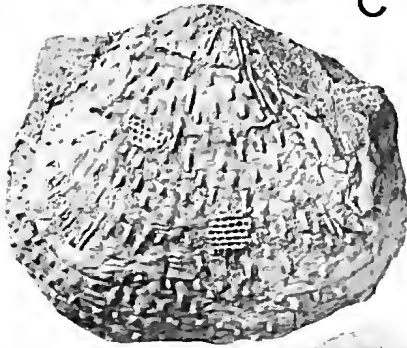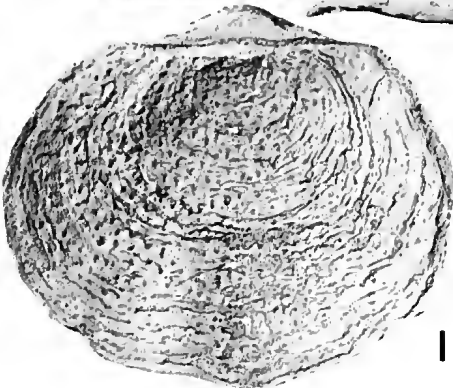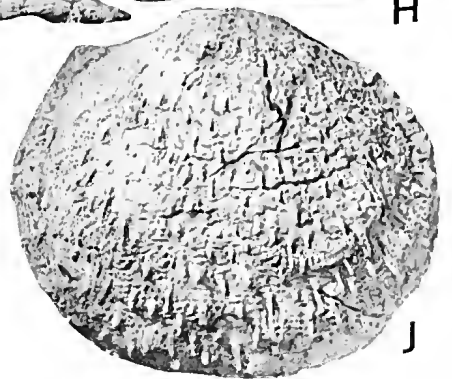
elongately oval in shape, smooth, bisected by median septum, moderately differentiated with anterior adductors being most prominent. Brachial ridges narrow, slightly to moderately elevated above disc floor, smooth. A distinct marginal ridge present in one dorsal interior, surrounding visceral disc. Numerous fine papillae present on floor of visceral disc with exception of brachial ridges and adductors, as well as on anterior trail where papillae may be arranged in distinct rows. Slight anterior thickening of dorsal valve occurs in all specimens available but varies in degree of development.

Discussion. The species was defined by Archbold (1986) on the basis of only four poorly preserved specimens, no isolated dorsal valves being available. The present study of topotypic material has confirmed characteristics of the species such as the large size at maturity, the weak ventral sulcus, and the strongly developed concentric lamellae and dimples on the dorsal valve.

The species was compared with allied forms by Archbold (1986: 102; 1991: 62).

Order ATHYRIDIDA Dagys, 1974
Superfamily ATHYRIDACEA McCoy, 1844
Family ATHYRIDIDAE McCoy, 1844

Genus Cleiothyridina Buckman, 1906

Type species. Atrypa pectinifera Sowerby, 1840.

Cleiothyridina ovalis Shi sp. nov.

Fig. 4A–P

Etymology. In reference to the oval outline of the species.

Holotype. GSWA F43896, a complete submature shell from GSWA locality F94218, Jimba Jimba Calcarenite, Carnarvon Basin.

Paratypes. GSWA F43894, one ventral valve, from GSWA locality F6252; GSWA F43895, a complete shell, from GSWA locality F6243; GSWA F43896–F43903, one complete shell and seven ventral valves, from GSWA locality 94218.

Size ranges. Maximum width: 21–46 mm; shell length: 21–32 mm; shell thickness: 8.2 mm (measured from holotype, the only one that appears not to have been crushed or distorted); ratio of shell length to width: 1

(immature)–0.84 (mature); width of ventral muscle field: 0.7–0.9 mm; length of ventral muscle field: 11–15 mm.

Diagnosis. Shells of small to medium size for genus; slightly transversely oval at maturity, gently plano-convex to gently concavo-convex in lateral profile; anterior commissure uniplicate; concentric growth lamellae pronounced, numbering 8–14 in 5 mm at midlength of mature specimens.

Description. Most specimens crushed and compressed to varying degrees but all appear to be gently plano-convex to gently concavo-convex in lateral profile. Outline slightly elongately oval in immature specimens, transversely oval at full maturity. Maximum width at midlength.

Ventral valve flat or gently concave in overall appearance although umbonal region usually gently swollen. Ventral umbo erect, moderately extended, truncated by small foramen of 1–2 mm diameter. Immature specimens almost lack sulcus, with nearly rectimarginate anterior commissure. Mature specimens with very gentle median depression which deepens particularly at anterior margin, giving rise to moderately strongly uniplicate anterior commissure. Dorsal valve gently to moderately convex, fastigium weakly developed, median fold results in uniplicate anterior commissure.

Concentric growth lamellae pronounced on both valves, numbering 8 in 5 mm at 8 mm from ventral umbo, 10 in 5 mm at midlength of shell, and 15 or more in 5 mm near anterior margin where a geniculate band 5–7 mm wide with crowded growth lamellae is observed in all large (mature) specimens. Presence of this geniculated band probably indicates full maturity of shells. Shell surfaces too abraded to preserve radial spines in most specimens, but traces of radial lines on lamellae present on some specimens.

Teeth robust, rounded, supported by dental plates which are fused into umbonal wall. Ventral muscle field relatively large, occupying third to almost half ventral valve floor, well differentiated into adductor and diductor scars. Adductor scars heart-shaped, located at posterior end of muscle field just below teeth, well depressed,

smooth, anteriorly passing onto low but prominent median ridge bisecting diductors. Diductor scars large, deeply depressed, separated from rest of valve floor by raised ridges, weakly striated. Remainder of valve floor marked by radial, in places anastomosing, vascular markings. Interior of dorsal valve unknown.

Discussion. The material is characterised by the low convexity, the ill-defined sulcus and the absence of a fold, and by the distinct uniplicate anterior commissure at maturity. These characteristics are also displayed by the specimens from the Callytharra Formation figured by Foord (1890) and Etheridge (1903) as *Cleiothyris* (= *Cleiothyridina*) *macleayana* (not Etheridge 1889), judged from their illustrations and descriptions. The type material of *Cleiothyridina macleayana* (Etheridge 1889: 208, pl. 17, figs 1–5) from the Baigendzhinian Noonkanbah Formation of the Canning Basin resembles the new species in size, outline and the anterior commissure but is clearly distinguished by its much more convex dorsal valve. The same is true of the comparison with *C. semiconcava* Waagen (1884: 481, pl. 41, figs 4–6) from the Late Artinskian to Kungurian Amb Formation of the Salt Range, Pakistan. The Salt Range species is further distinguished by its more strongly folded anterior commissure. *C. roysii* var. *penta* Prendergast (1935: 24, pl. 2, figs 13–15) from the Luiluigui Station, Kimberley Division, approaches the new species in size and particularly in its flat to gently concave ventral valve, but this species is pentagonal in outline and has a high dorsal valve and a deep, well pronounced sulcus and strongly uniplicate anterior commissure. *C. baracoodensis* (Etheridge 1903: 17, pl. 3, figs 5–9) from the Callytharra Formation of the Carnarvon Basin is distinguished from the new species by its gently to moderately convex ventral valve and more inflated dorsal valve.

Cleiothyridina seriata Grant (1976: 199, pl. 53, figs 1–30, pl. 54, figs 1–62, text-fig. 18) from the Baigendzhinian or Kungurian fauna of the Rat Buri Limestone in south Thailand is smaller in size, more rounded in outline, and moderately biconvex in profile in comparison with *C. ovalis*. Another species figured as *Cleiothyridina* sp. from the Sterlitamakian fauna of the Ka Yao Noi Formation of south Thailand (Waterhouse et al. 1981) is also small and little inflated like the Jimba Jimba material. The Thai form was said to be immature and thus cannot be identified or compared with any named species with certainty, but it differs from *C. ovalis* in being rounded in outline rather than elongately oval or transversely oval.

Order SPIRIFERIDA Waagen, 1883
Superfamily SPIRIFERACEA Waagen, 1883
Family SPIRIFERIDAE King, 1846
Subfamily NEOSPIRIFERINAE Waterhouse, 1968

Genus **Crassispirifer** Archbold & Thomas, 1985

Type species. Spirifer rostalinus Hosking, 1931.

Crassispirifer condoni Archbold & Shi sp. nov.

Fig. 7A–N

Etymology. For Mr M. A. Condon, who first proposed and mapped the Jimba Jimba Calcarenite in the Carnarvon Basin.

Holotype. CPC 31493, a complete specimen with valves conjoined, from BMR locality WO3.

Paratypes. CPC 31493–31496, a complete shell, two dorsal valves and one ventral valve from BMR locality WO3. GSWA F43912–F43917, four ventral valves and two dorsal valves, all incomplete, from GSWA locality F6243.

Size ranges. Maximum width: usually 40–70 mm, rarely up to 90 mm; height: 18–32 mm; thickness
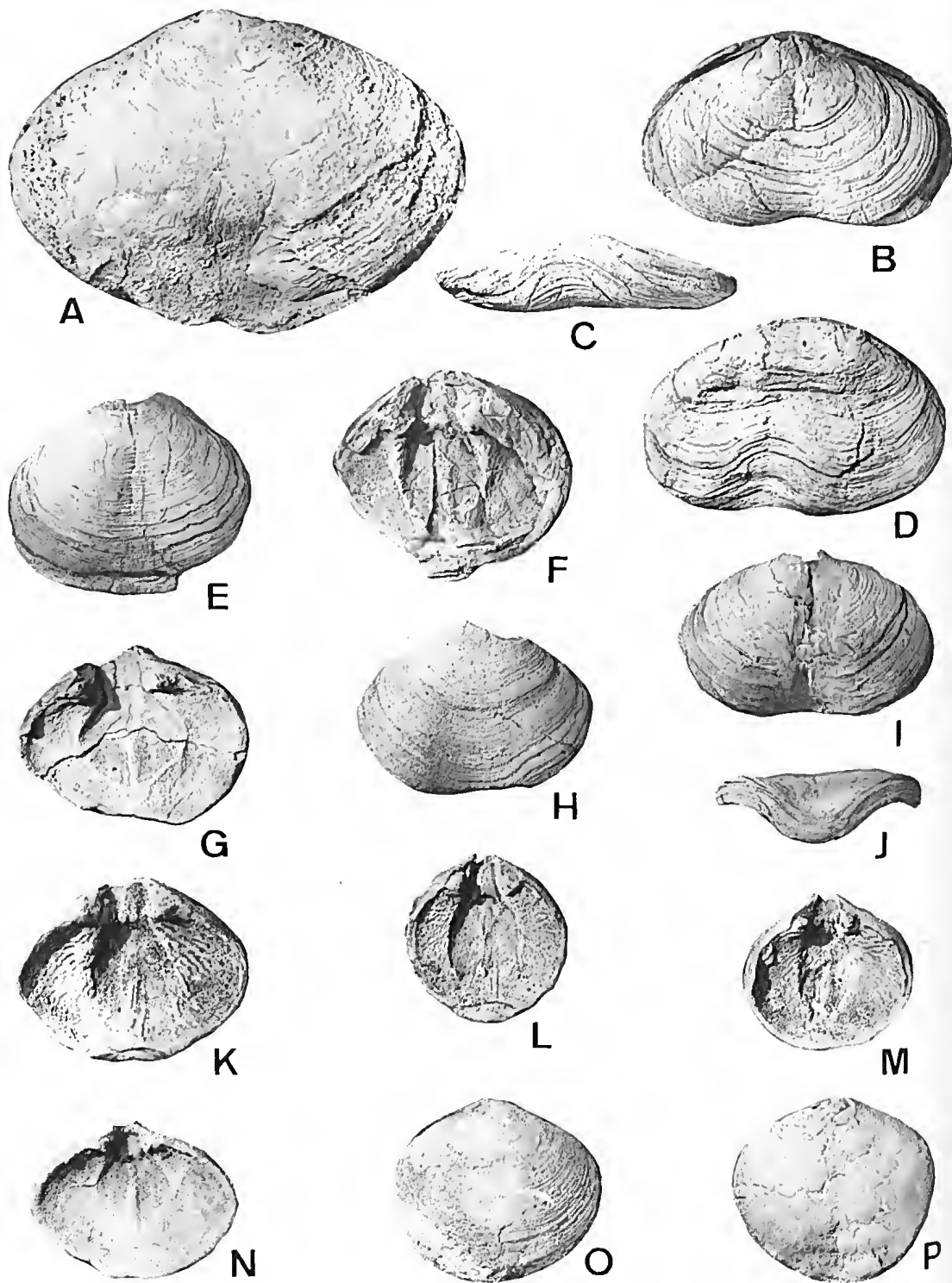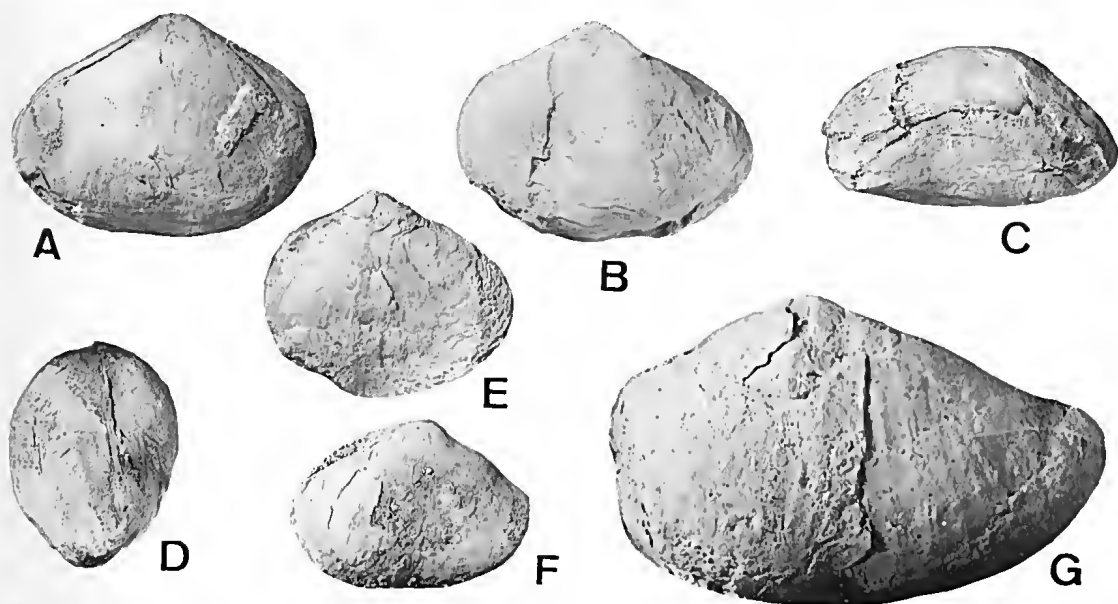
Fig. 5. Cleiothyridina cf. *C. baracoodensis* (Etheridge). A–D, GSWA F43904, from locality F6253, decorticated shell in ventral, dorsal, anterior and lateral views, × 1.22. E, GSWA F43906, from locality F6252, decorticated ventral valve in ventral view, × 1.2. F, GSWA F43907, from locality F6254, decorticated ventral valve in ventral view, × 1.2. G, GSWA F43905, from locality F6254, decorticated ventral valve in ventral view, × 2.5.

(measured from holotype only): 22 mm; width/height ratio: 2.5–2.9; dorsal valve height: 16–22 mm; ventral interarea height: 5–10 mm; dorsal interarea height: 2?–3 mm.

Diagnosis. Small, moderately convex *Crassispirifer* with broad and shallow sulcus and moderately high, well rounded fastigium. Lateral plicae weak to distinct. Costae equidimensional and low. Anterior sulcal tongue short.

Description. Shell transverse in outline with well extended cardinal extremities; widest at hinge margin.

Ventral valve moderately convex. Umbo small, moderately extended and incurved; umbonal slopes gently concave. Interarea low and wide, marked by both horizontal and vertical striations, divided by relatively large delthyrium; delthyrial plate unknown. Sulcus commences from umbo, initially defined by pair of prominent costae which at 8 to 10 mm from umbo become incorporated onto sulcal slopes; sulcus defined anteriorly by pair of plicae. Sulcus narrow and shallow over posterior third of ventral valve length, widens and deepens anteriorly towards anterior margin; sulcal floor broadly U-shaped in cross-section, terminates at front in short, rounded sulcal tongue. Lateral slopes gently convex, each bearing at least three low, indistinct plicae. Costae initially sharply defined, fine, equidimensional; anteriorly costae become relatively coarse and flattened,

Fig. 4. Cleiothyridina ovalis Shi sp. nov. A, GSWA F43894, ventral valve in ventral view, × 2.5. B–D, GSWA F43896, holotype, crushed shell in ventral, anterior and dorsal views, × 1.2. E, F, GSWA F43897, ventral valve in ventral and interior views, × 1.2. G, H, GSWA F43898, ventral valve in interior and ventral views, × 1.2. I, J, GSWA F43899, ventral valve in ventral and anterior views, × 1.2. K, GSWA F43900, ventral valve interior view, × 1.2. L, GSWA F43901, ventral valve interior view, × 1.2. M, GSWA F43902, ventral valve interior view, × 1.2. N, GSWA F43903, ventral valve interior view, × 1.2. O, P, GSWA F43895, shell in dorsal and ventral views, × 1.2.
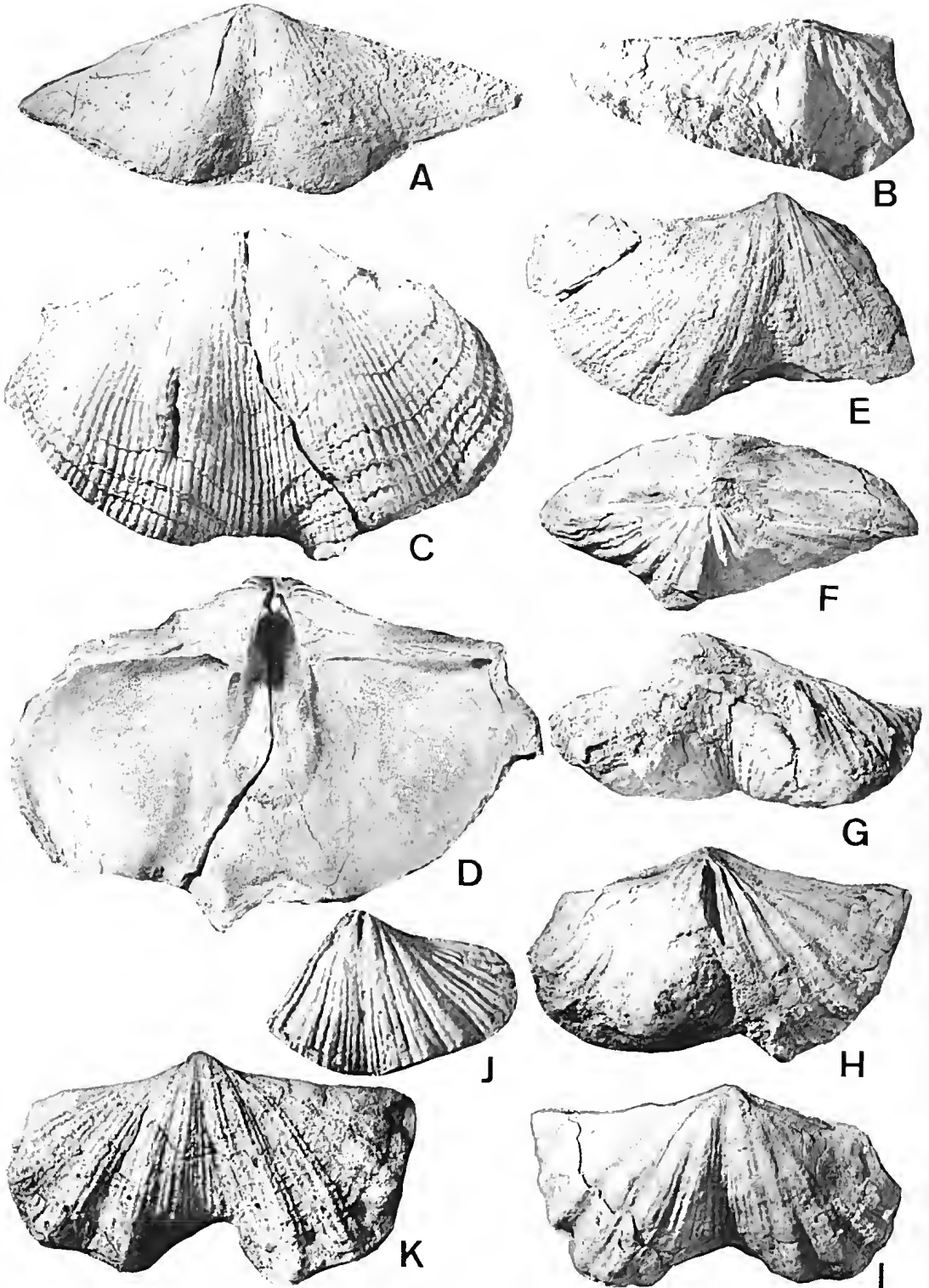
Fig. 6. A, B, *Cyrtella* sp. A, GSWA F43908, from locality F94218, ventral valve in ventral view, × 1. B, GSWA F43909, from locality F6254, dorsal valve in dorsal valve, × 1.5. C–E, J, *Neospirifer hardmani* (Foord). C, D, CPC 31490, ventral valve in ventral view, × 1. E, GSWA F43910, from locality F6255, ventral valve in ventral view, × 1. J, GSWA F43911, from locality F6256, juvenile ventral valve in ventral view, × 2. F–I, K, *Neospirifer* cf. *N. foordi* Archbold & Thomas. F–I, CPC 31491, shell in posterior, anterior, dorsal and ventral views, × 1. K, CPC 31492, ventral valve in ventral view, × 1.

between 0.8–1 mm wide. Median sulcal costa ill-defined, fine.

Dorsal valve of similar convexity to ventral valve; umbo small and low. Fastigium well differentiated from gently convex lateral slopes by low lateral depressions, generally low over posterior third of valve length, strongly elevated at front, giving rise to high, well rounded fold. Lateral plicae low and indistinct. Costae fine, equidimensional, numbering 5–6 in 5 mm at frontal margin.

Shell micro-ornament consists of prominent fine growth lamellae and poorly preserved capillae, with lamellae numbering 3–6 per mm and, on some specimens, crowded together to form broad growth steps, especially towards anterior margin.

Dental flanges stout, thickened, with prominent delthyrial ridges. Adminicula thickened and entirely buried in posterior shell thickening. Ventral muscle field longer than wide, deeply depressed below valve floor. Dorsal interior unknown.

Discussion. In outline, convexity, plication and sulcal details, the new species is similar to presumed juvenile specimens of *Fusispirifer carnarvonensis* Archbold & Thomas (1987: 177, figs 1E–F, 2D, F) from the Sterlitamakian Callytharra Formation but differs from those specimens in its higher fastigium, deeper sulcus and generally better defined lateral plicae. *Crassispirifer condoni* sp. nov. probably represents a small ancestral species of *Crassispirifer*, as indicated by its relatively robust shell and the development of extended anterior growth resulting in a trigonal shell outline. Other species assigned to *Crassispirifer* are larger and more subquadrate in outline and possess stronger lateral plications, broader sulci and higher fastigia (Archbold & Thomas 1985).

ACKNOWLEDGEMENTS

REFERENCES

ARCHBOLD, N. W., 1981. Studies on Western Australian Permian brachiopods 2. The family Rugosochonetidae Muir-Wood, 1962. *Proceedings of the Royal Society of Victoria* 93: 109–128.

ARCHBOLD, N. W., 1982. *Sommeriella*, a new name for the Permian chonetacean brachiopd subgenus *Sommeria* Archbold, 1981. *Proceedings of the Royal Society of Victoria* 94: 10.

ARCHBOLD, N. W., 1983. Studies on Western Australian Permian brachiopods 3. The family Linoproductidae Stehli, 1954. *Proceedings of the Royal Society of Victoria* 95: 237–254.

ARCHBOLD, N. W., 1986. Studies on Western Australian Permian brachiopods 6. The genera *Strophalosia* King, 1844, *Heteralosia* King, 1938 and *Echinalosia* Waterhouse, 1967. *Proceedings of the Royal Society of Victoria* 98: 97–119.

ARCHBOLD, N. W., 1991. Studies on Western Australian Permian brachiopods 10. Faunas from the Wooramel Group, Carnarvon Basin. *Proceedings of the Royal Society of Victoria* 103: 55–66.

ARCHBOLD, N. W. & THOMAS, G. A., 1985. New genera of Western Australian Spiriferidae (Brachiopoda). *Alcheringa* 9: 269–292.

ARCHBOLD, N. W. & THOMAS, G. A., 1986a. *Neospirifer* and *Trigonotreta* (Spiriferida, Brachiopoda) from the Permian of Western Australia. *Alcheringa* 10: 125–61.

ARCHBOLD, N. W. & THOMAS, G. A., 1986b. Permian Ingelarellidae (Brachiopoda) from Western Australia and Argentina. *Journal of Paleontology* 60: 581–605.

ARCHBOLD, N. W. & THOMAS, G. A., 1987. *Fusispirifer* (Spiriferida, Brachiopoda) from the Permian of Australia and Afghanistan. *Alcheringa* 11: 175–203.

BUCKMAN, S. S., 1906. Brachiopod nomenclature. *Annals and Magazine of Natural History, Series 7*, 18: 321–327.

COCKBAIN, A. E., 1966. Palaeontology of Samples from the Kennedy Range Damsite. Geological Survey of Western Australia Palaeontological Report 62/66, 10 p. (unpublished).
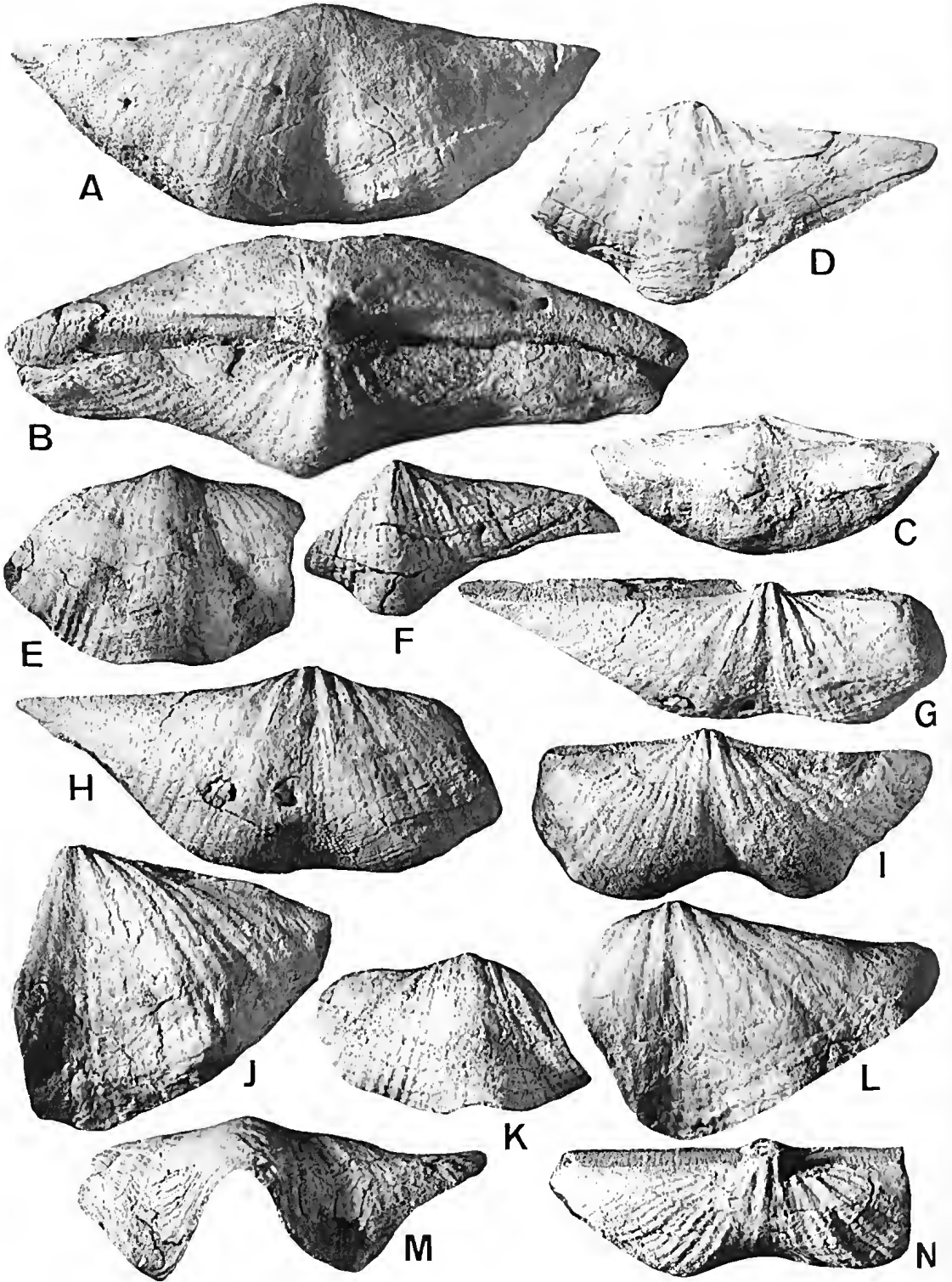
Fig. 7. Crassispirifer condoni Archbold & Shi sp. nov. A–C, CPC 31493, holotype, shell in ventral, posterior and dorsal views, × 1.6, × 2 and × 1. D, M, CPC 31494, dorsal valve in dorsal and anterior views, × 1.3. E, GSWA F43916, dorsal valve in dorsal view, × 1.3. F, CPC 31495, dorsal valve in dorsal view, × 1.3. G, H, CPC 31496, ventral valve in posterior and ventral views, × 1.4. I, GSWA F43912, ventral valve in posteroventral view, × 1.3. J, GSWA F43913, ventral valve in ventral view, × 1.3. K, GSWA F43917, dorsal valve in dorsal view, × 1.3. L, GSWA F43914, ventral valve in ventral view, × 1.3. N, GSWA F43915, ventral valve in posterior view, × 1.3.
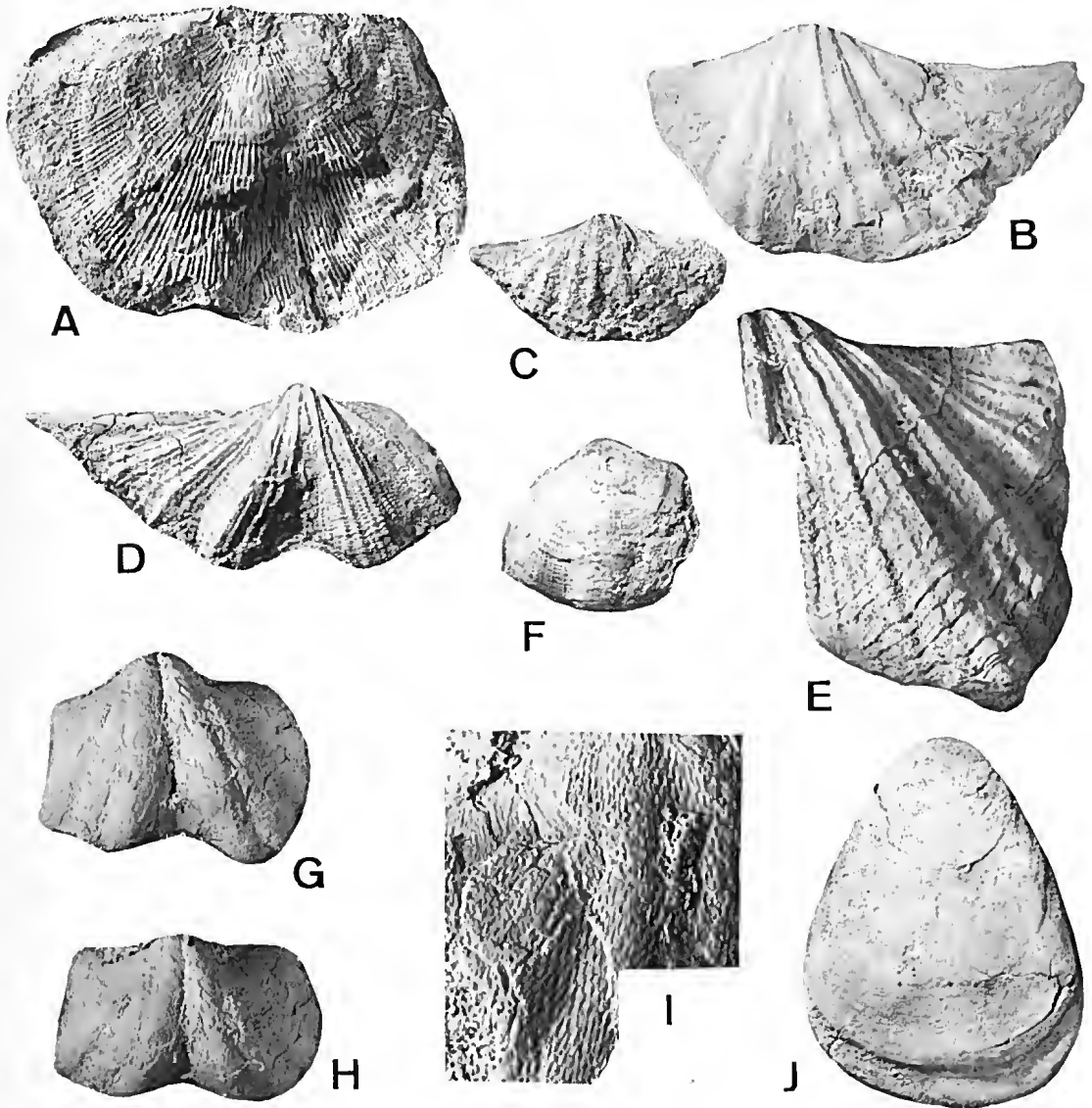
Fig. 8. A, *Permorthotetes* cf. *P. lindneri* Thomas, GSWA F43870, from locality F6248, ventral valve in ventral view, × 1. B–E, *Trigonotreta neoaustralis* Archbold & Thomas. B, GSWA F49056, from locality F6253, ventral valve in ventral view, × 1.3. C, CPC 31497, ventral valve in ventral view, × 1. D, CPC 31498, ventral valve in ventral view, × 1.5. E, GSWA F49057, from locality F6244, ventral valve in ventral view, × 1. F, *Spirelytha* sp., GSWA F49058, from locality F6248, dorsal valve in dorsal view, × 1. G–I, *Tomiopsis* cf. *T. rarus* Archbold & Thomas, GSWA F49059, from locality F6243, ventral valve in ventral and posterior views, × 1.6, and micro-ornament enlarged, × 8. J, *Hoskingia*? sp., CPC 31499, ventral valve in ventral view, × 1.1.

COCKBAIN, A. E., 1980. Permian ammonoids from the Carnarvon Basin—a review. *Geological Survey of Western Australia Annual Report for 1979*, Perth, 100–105.

CONDON, M. A., 1965. *1:250,000 Geological Series Explanatory Notes, Wooramel, WA, Sheet SG/50-5, International Index.* Bureau of Mineral Resources, Geology and Geophysics, Canberra, 20 p.

CONDON, M. A., 1967. The geology of the Carnarvon Basin, Western Australia, part 2. Permian stratigraphy. *Bureau of Mineral Resources, Geology and Geophysics Bulletin* 77: 1–190.

DAVIDSON, T., 1859. Palaeontological notes on the Brachiopoda. No. 2. On the families Strophomenidae and Productidae. *The Geologist* 2: 97–117.

DICKINS, J. M., 1963. Permian pelecypods and gastropods from Western Australia. *Bureau of Mineral Resources, Geology and Geophysics Bulletin* 63: 1–202.

ETHERIDGE, R., 1889. Remarks on fossils of Permo-Carboniferous age, from north-western Australia, in the Macleay Museum. *Proceedings of the Linnean Society of New South Wales* 4: 199–214.

ETHERIDGE, R., 1903. Descriptions of Carboniferous fossils from the Gascoyne district, Western Australia. *Geological Survey of Western Australia Bulletin* 10: 7–31.

FOORD, A. H., 1890. Notes on the palaeontology of Western Australia. Carboniferous fossils from the Gascoyne River and its vicinity. *Geological Magzine, Decade 3,* 7: 145–155.

GLENISTER, B. F. & FURNISH, W. M., 1961. The Permian ammonoids of Australia. *Journal of Paleontology* 35: 673–736.

GRANT, R. E., 1976. Permian brachiopods from southern Thailand. *Paleontological Society Memoir* 9: 1–269.

HOCKING, R. M., MOORS, H. T. & VAN DE GRAAFF, W. J. E., 1987. Geology of the Carnarvon Basin, Western Australia. *Geological Survey of Western Australia Bulletin* 133: 1–289.

HOSKING, L. V. F., 1931. Fossils from the Wooramel district, Western Australia. *Journal of the Royal Society of Western Australia* 17: 7–52.

KING, W., 1844. On a new genus of Palaeozoic shells. *Annals and Magazine of Natural History* 14: 313–317.

KING, W., 1846. Remarks on certain genera belonging to the class Palliobranchiata. *Annals and Magazine of Natural History* 18: 26–42, 83–94.

MUIR-WOOD, H. M., 1962. *On the Morphology and Classification of the Brachiopod Suborder Chonetoidea.* British Museum (Natural History), London, 132 p.

PALMIERI, V., 1990. Permian Foraminifera of Australia. *Tenth Australian Geological Convention. Geological Society of Australia Abstracts*, No. 25, 53–54.

PLAYFORD, P. E., COPE, R. E., COCKBAIN, A. E., LOW, G. H. & LOWRY, D. C., 1975. Phanerozoic. *Geological Survey of Western Australia Memoir* 2: 223–436.

PRENDERGAST, K. L., 1935. Some Western Australian Upper Palaeozoic fossils. *Journal of the Royal Society of Western Australia* 21: 9–35.

PRENDERGAST, K. L., 1943. Permian Productinae and Strophalosiinae of Western Australia. *Journal of the Royal Society of Western Australia* 28: 1–73.

RUNNEGAR, B. N., 1969. The Permian faunal succession in eastern Australia. *Geological Society of Australia Special Publication* 2: 73–98.

SOWERBY, J. DE C., 1840. *The Mineral Conchology of Great Britain*, vol. 7, London, 80 p.

THOMAS, G. A., 1958. The Permian Orthotetacea of Western Australia. *Bureau of Mineral Resources, Geology and Geophysics Bulletin* 39: 1–159.

THOMAS, G. A., 1969. The Permian brachiopod faunas of Western Australia. In *Gondwana Stratigraphy* (IUGS Symposium), UNESCO, Paris, 217–234.

VAN DE GRAAFF, W. J. E., HOCKING, R. M. & DENMAN, P. D., 1977. Revised stratigraphic nomenclature and interpretations in the east-central Carnarvon Basin, WA. *Annual Report of the Geological Survey of Western Australia for 1976*, Perth, 37–39.

WAAGEN, W., 1884. Salt Range fossils. Part 4. Brachiopoda. *Memoirs of the Geological Survey of India, Palaeontologia Indica, Series 13*, 2–4: 391–728.

WATERHOUSE, J. B., 1970. Gondwanan occurrences of the Upper Palaeozoic brachiopod *Stepanoviella. Journal of Paleontology* 44: 37–50.

WATERHOUSE, J. B., PITAKPAVIAN, K. & MANTAJIT, N., 1981. Early Permian brachiopods from Ko Yao Noi and near Krabi, southern Thailand. *Geological Survey of Thailand Memoir* 4: 47–146.

PROCEEDINGS

OF THE

ROYAL SOCIETY OF VICTORIA

Volume 106

CONTENTS OF VOLUME 106

THE SPATANGOID ECHINOID *LOVENIA* FROM THE TERTIARY OF SOUTHEASTERN AUSTRALIA

R. P. Irwin & N. W. Archbold

School of Aquatic Science and Natural Resources Management, Deakin University, Rusden Campus, 662 Blackburn Road, Clayton, Victoria 3168

Irwin, R. P. & Archbold, N. W., 1994:12:31. The spatangoid echinoid *Lovenia* from the Tertiary of southeastern Australia. *Proceedings of the Royal Society of Victoria* 106: 1–15. ISSN 0035-9211.

A study of three localities in the Tertiary of southeastern Australia revealed that the spatangoid echinoid *Lovenia* Desor is represented by the species *L. forbesii* (Woods, 1862), *L. woodsii* (Etheridge, 1875) and *L. bagheerae* sp. nov. A preliminary qualitative study of the three species demonstrated the changes that occur during ontogeny.

TERTIARY marine strata are developed widely in southeastern Australia in major basins including the Murray, Otway, Bass and Gippsland basins (Fig. 1). Reviews of the stratigraphy of these deposits were provided by Singleton (1968), Darragh (1985), Mallett & Holdgate (1985) and Abele et al. (1988). These reviews also provide details of the local southeastern Australian stage terminology and the correlation of stratigraphical sections and stages with Australian and international planktic foraminiferal zones. Truswell et al. (1991) provide the most recent survey of international correlations for the Australian Tertiary successions.

Details of stratigraphical units (formations), localities and ages of the strata yielding the collections for the present study are provided with the descriptions of the species; general localities are shown on Fig. 1.

Usage of specific names. There has been considerable confusion regarding authorship of *Spatangus forbesii*. The specific name was originally attributed by Woods (1859) to specimens from Portland and Mt Gambier and later applied by Woods (1860, 1862) to specimens reputed to be from Mt Gambier. Of the illustrated account (1862: 75, 83), the second figure, is a reproduction of Sturt's (1833: pl. 3)
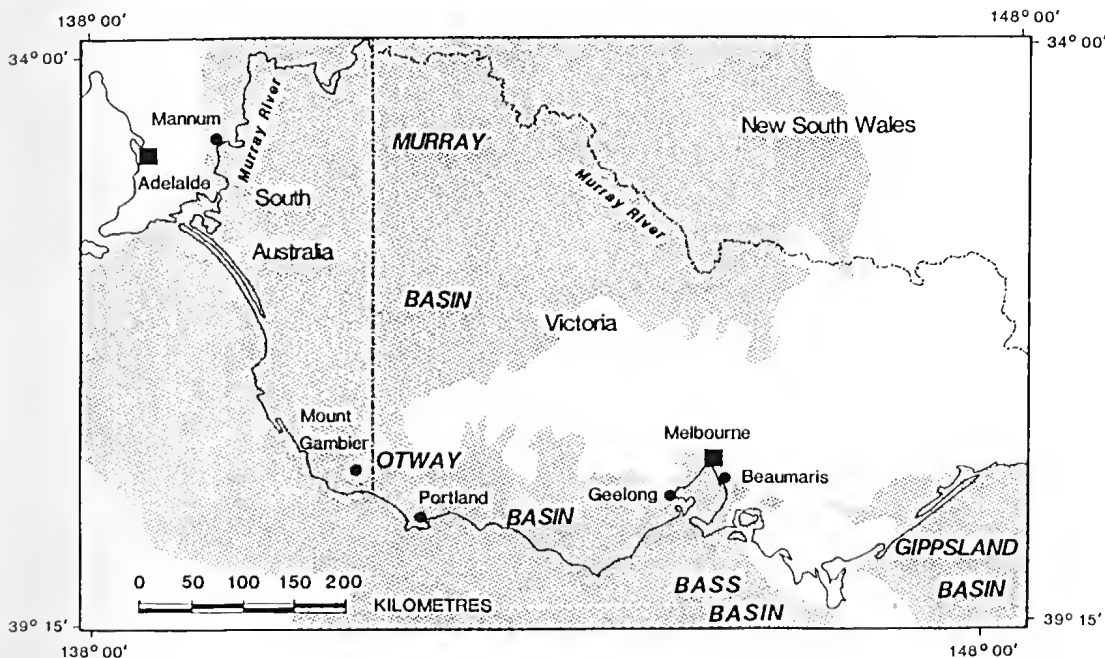
Fig. 1. Distribution of Tertiary marine strata in southeastern Australia and general localities mentioned in text.

Murray River cliffs specimen. Despite the absence of a formal diagnosis, Woods' illustrated account (1862) appears to satisfy the provisions of the International Code of Zoological Nomenclature for the validity of the specific name and authorship. Subsequently, Etheridge (1875) recognised *L. woodsii* from Beaumaris. This species was invariably synonymized by later workers with *L. forbesii*, and it was not until midway through the twentieth century (Pritchard 1976; paper actually written in 1947) that *L. woodsii* was again recognized as a distinct species. Nevertheless confusion over the use of specific names has persisted.

The Portland population of *Lovenia* investigated for this study has previously been assigned to both *L. woodsii* (e.g. Carter 1963; Singleton 1968; Abele et al. 1988) and *L. forbesii* (Murray 1985) without critical investigation but is shown by us to represent a distinctive new species.

SYSTEMATIC PALAEONTOLOGY

Terminology used in the descriptions below is that of Melville & Durham (1966).

All material is housed in the Department of Invertebrate Palaeontology, Museum of Victoria.

Class ECHINOIDEA Leske, 1778

Order SPATANGOIDA Claus, 1876

Family LOVENIIDAE Lambert, 1905

Genus **Lovenia** Desor, 1847

Type species.   Spatangus elongatus Gray, 1845.

Diagnosis.   See Fischer (1966).

Lovenia forbesii (Woods, 1862)

Fig. 2

Spatangus Hoffmanni, Goldfuss.—Sturt 1833: 254, pl. 3, fig. 10.
Spatangus Forbesii Woods 1862: 83.
Spatangus Forbesi, Woods.—Duncan 1864: 165, ? pl. 6, fig. 3.
Hemipatagus Forbesi, Woods & Duncan.—Duncan 1864: 165, ? pl. 6, figs 3–? Woods 1867b: 1–2, fig. 3.
Hemipatagus Forbesii, Woods & Duncan.—Woods 1867a: 1.—Duncan 1870: 285.
Hemipatagus Forbesii, Woods sp.—Laube 1869: 193–194, fig. 4.

Lovenia Forbesi, Woods & Duncan.—Duncan 1877: 44, 56–61, pls 4/5–8.
Lovenia Forbesi var. *Woodsi*, Etheridge.—Duncan 1877: 44, 56–61, 63, pl. 4, figs 5–8.
Lovenia Forbesii, Woods & Duncan.—Etheridge 1878: 141.—Woods 1878: 76.
Lovenia Forbesii, var. *Woodsii*, Etheridge.—Etheridge 1878: 141.
Lovenia Forbesi, McCoy.—McCoy 1879: 37–40, pl. 60, figs 1–4.
Lovenia Forbesii, Woods.—Tate 1885: 37, 39, 41.
Lovenia Forbesi.—Tate 1885: 34.
Lovenia Forbesi, var. *Woodsii*, Etheridge.—Johnston 1887: 130.
Lovenia Forbesi, Duncan.—Pritchard 1892: 186.
Lovenia Forbesi, Woods.—Tate & Dennant 1893: 226.
Lovenia forbesi.—Brown 1910: 4.—Ludbrook 1957: 178.—Ludbrook 1958: 108–110.—Ludbrook 1961: 38, 43, table 1.—Ludbrook 1969: 180.—McNamara 1991b: 42, figured, 43, figured, 44.
Lovenia forbesi, Woods.—Chapman 1914: 147, 150.—Chapman 1915: 44.—Howchin 1928: 402–403, fig. 172/c.—Ludbrook 1961: 44, 45, 48, 60, 62, pl. 8, figs 5, 6, table 1.—Sadler, Pledge & Morris 1983: 25.—McNamara & Ah Yee 1989: 177.
Lovenia forbesii, Woods.—Philip 1963: 184.—Archbold 1990: 119, figs A, C.
Lovenia forbesi, Woods & Duncan.—Aslin 1980: 9, figs 5–8.—Holmes 1987: 33, fig. 4.
Lovenia forbesii.—Abele 1988: pl. 4-1/b, c.
Lovenia.—Brown & Stephenson 1991: 429.

Lectotype.   The location of both Sturt's and Wood's original specimens are unknown therefore in the interests of nomenclatural stability, the specimen figured by Sturt, pl. 3, fig. 10, and redrawn by Woods, p. 83, is herein selected as lectotype according to ICZN 3rd edn. Article 74(c). The specimen is from the fossiliferous Murray River cliffs of South Australia, believed to be the Early Miocene (Longfordian) Mannum Formation.

Material and locality.   NMV P78919–P78957, 34 specimens from the Longfordian (Aquitanian–Burdigalian) Mannum Formation, Murray Basin with the general location Murray cliffs were examined, excluding NMV P78927, P78935, P78941, P78943, P78951 which are from the Port Campbell Limestone at Portland and are here assigned to *L. bagheerae* sp. nov.).

Size ranges.   Length 14.2–36.6 mm; width 12.9–34.4 mm; height 6.9–19.6 mm; width as % of test length 87–96%; (mean 91%); height as % of test length 45–56%; (mean 50%).

Diagnosis.   Test distinctly heart-shaped with maximum width less than half-way from anterior end. Shallow anterior sulcus. Large number of primary tubercles, extending into posterior half of test;

Fig. 2.   A–K, *Lovenia forbesii* Woods. All figures ×2. A, C, NMV P78929, lateral and posterior views; B, G, NMV P78946, adapical and adoral views; D, E, H, K, NMV P78919, adoral, posterior, adapical and lateral views; F, I, J, NMV P78937, adapical, posterior and adoral views.
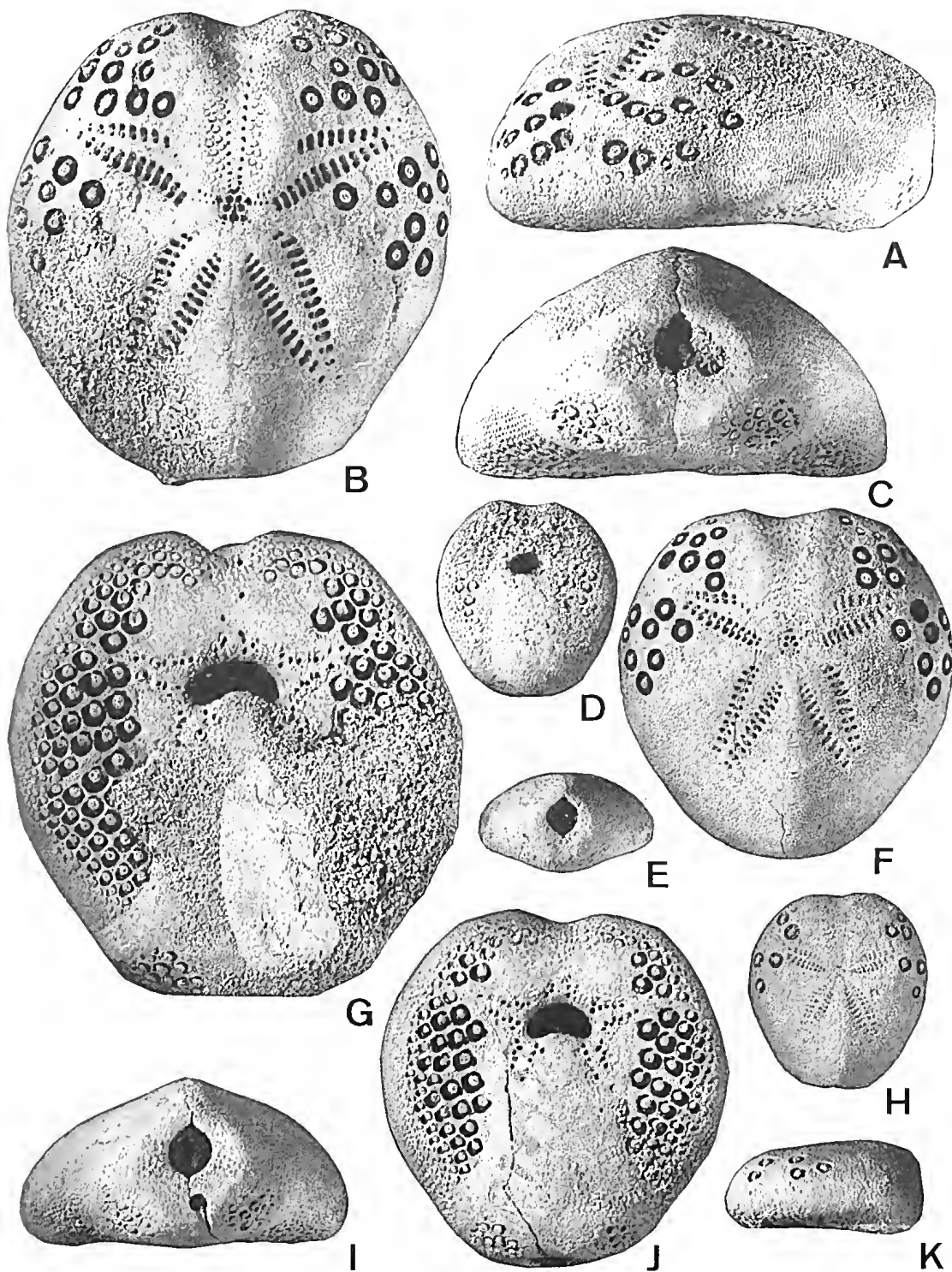
frequently in interambulacra 2a/3b. Antero-lateral petals terminate half way to ambitus, equal in width and length to posterior petals, ambulacra IIb/IVa ½–⅓ length of IIa/IVb. Periproct elongated in dorso-ventral plane, peristome antero-posteriorly broad.

Remarks.   Both Duncan (1877) and McCoy (1879) included a combination of characters now known to embrace both *L. forbesii* and *L. woodsii*. McCoy (1879) recognised that the Murray cliffs specimens differed from those near Melbourne by possessing a greater number of tubercles, a less pentagonal test and a more anteriorly positioned apex. Nevertheless, he and Duncan (1877) considered *L. forbesii* to be highly variable. McCoy also considered that *L. forbesi* var. *minor* (Duncan 1877) exceeded the difference in variation, and so lacked validity.

Forbes (1852) reported on echinoids from the Murray River and *Spatangus* from Melbourne. His figure b, on page 50 is labelled *Spatangus*, implying Melbourne as the locality, yet the test outline and large peristome resembles *L. forbesii*. Duncan (1864) described *L. forbesii* from the Murray River cliffs and Mount Gambier, the figure resembling *L. bagheerae* sp. nov.

Woods (1867b) figured *Hemipatagus forbesi* from either the Murray River or Mount Gambier, but many attributes depicted are inconsistent with the three *Lovenia* species described herein and so it cannot be identified. Laube (1869) also figured *L. forbesii* but this is considered inaccurate regarding characteristics of the sulcus and ambulacral columns.

Through discovery of the internal fasciole, Duncan (1877) transferred *H. Forbesi* to *Lovenia*, supplying four figures of specimens from the Murray cliffs, Mount Gambier, Mordialloc (Beaumaris) and the Hamilton Tertiaries (probably a Port Campbell Limestone equivalent). Three of the figures combine attributes of specimens derived from these different localities.

McCoy (1879) supplied four figures of *L. forbesi* (*sic*) based on specimens collected from similar localities as Duncan (1877) but with the addition of Torquay; figs 1 and 2 strongly resembling *L. woodsii*. Despite studying hundreds of specimens, McCoy reported that only one to three rows of primary tubercles develop in interambulacra 2a and 3b, yet four are common in all large specimens. The statement of two to five rows on the anterior part of the postero-lateral interambulacra suggests that the tubercles remain in the anterior half of the test, unlike *L. forbesii*.

In light of these inconsistencies, those descrip-

tions by Duncan (1864, 1877) and McCoy (1879) are regarded inaccurate.

Species differentiation.   The presence of primary tubercles in interambulacral columns 1a and 4b, a heart-shaped test, dorso-ventrally elongated periproct (Fig. 3) and anterior petals extending only half way to ambitus are unique to *L. forbesii*.
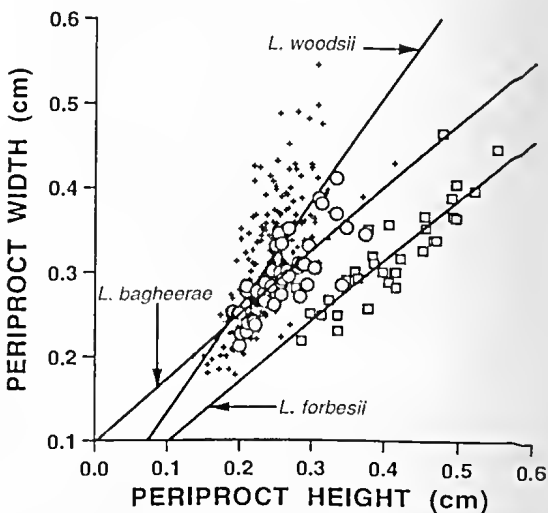
Fig. 3.   Bivariate plot of periproct height vs. periproct width indicating intermediate nature of *L. bagheerae* sp. nov. (○) periproct as compared to horizontally and vertically elongate periprocts of *L. woodsii* (+) and *L. forbesii* (□) respectively.

Description.   Test reaches a maximum known length of 50 mm; widest slightly anterior to mid-test length, resulting in heart shaped test. Width varies between 87–96% TL. Anterior test margin rises abruptly to internal fasciole, levelling out toward apical system, keel elevated immediately posterior to apical system, declining thereafter to posterior margin. Maximum height generally immediately posterior of apical system, however larger specimens have swollen ambulacrum III producing greatest height anterior of apical system. Height varies between 45–56% TL. Test has broad shallow anterior sulcus.

Apical system tetrabasal; tilted anteriorly, located about 40% TL of anterior; ethmolytic with four genital pores, smaller anterior pair closer than posterior; asymmetry of genital pores, left pair larger than right; madreporite oblanceolate, extending just posterior of ocular plates I, V; ocular pores very minute.

Adapically, ambulacrum III sunken, progressively deepening adorally, attenuating adapically, forming sulcus with peripheral coarse miliary tubercles of interambulacra 2b, 3a; ambulacrum bears minute adradial conjugate pores, size increasing adorally; more adoral pore displaced slightly perradial of adapical pore; pore pairs become more widely spaced adorally.

Antero-lateral ambulacral petals broad adapically, contracting abapically, terminating just over half-way to ambitus; anterior row of large pore pairs ½–⅔ length of posterior row; large pore pairs run almost transversely, smaller pore pairs subparallel to posterior row; angle of divergence of ambulacra IIb, IVa small pore pairs about 90°. Posterior row commonly straight, occasionally adapical half gently curved; terminates closer to apical system than anterior row; small pore pairs intersect apical system transversely; posterior rows diverge anteriorly at about 130°. Large pore pairs in petals conjugate, deeply recessed, anterior row reduced; adradial pore of each column more adoral, varying from similar in size to twice that of perradial pore; shape varies from orbicular to ovate with apex inclined adapically; pores closest to ambitus and apical system smallest; 9–13 pore pairs in column IIa, mean 11.2; 10–14 in IVb, mean 11.7; 4–9 in IIb, mean 6.5; 4–9 in IVa, mean 6.9; asymmetry with more pore pairs on left side of test.

Posterior ambulacral petals as wide as antero-lateral petals, terminate half-way to ambitus, both rows slightly sinuous, equal in length, divided anteriorly, merging posteriorly; angle of divergence of rows about 60°; ambulacra Ib, Va small pore pairs meet almost transversely. Large pore pairs commonly smaller or conjugates closer than in antero-lateral petals; 11–16 pore pairs in column Ia, mean 12.7; 11–15 in Vb, mean 13.2; 10–14 in Ib, mean 12.1; 10–15 in Va, mean 12.4; anterior rows shorter than posterior rows; asymmetry with more pore pairs on left side of test. Two aberrant specimens (NMV P78940, P78947) possess three pores in some plates of ambulacra I and V; extra pore small, orbicular, central between conjugate pores, displaced abapically.

Primary tubercles of adapical surface with perforate circular mamelon, flush with extrascrobicular surface, neck straight, platform impressed, surrounded by noncrenulate parapet; boss passes down imperceptibly into deep scrobicle; occasionally scrobicles coalesce near ambitus, rarely more adapically; tubercles absent from interambulacrum 5, occasionally occurring in 2b, 3a, more common in larger specimens; 0–1 primary tubercle in 2b, 3a, mean 0.2; échelon arrangement in Ib–2a and 3b–4a with tubercles sloping interradially down-

ward, 1 to 4 rows per column; 3–13 primary tubercles in Ib, mean 7.8, 3–11 in 4a, mean 7.1; 3–13 in 2a, mean 8.0; 3–13 in 3b, mean 7.3; asymmetry with more primary tubercles on right side of test; tubercles present in anterior portion of 1a and 4b; 0–3 in Ia, mean 1.3; 0–3 in 4b, mean 1.4; asymmetry reversed compared to anterior half of test.

Primary tubercles of adoral surface confined to lateral margins; mamelon projects above extrascrobicular surface; scrobicle enlarged posterior of mamelon, boss confluent with anterior margin of scrobicle (Fig. 4C); tubercle size decreases adapically; tubercles of interambulacrum 5 restricted to dilated ends of spectacle-shaped fasciole (Fig. 4B), comparable in size to more ambital adoral tubercles, boss confluent with adapical margin of scrobicle; interambulacra 1, 4 tubercles occupy lateral region one-third of test width; tubercles of interambulacra 2, 3 restricted to ambital margin.

Entire apical surface granulated with close fine miliary tubercles; very minute granules comprise narrow internal fasciole (Fig. 4A); beginning just posterior of apical system perpendicular to posterior petals, forming obtuse angle, intersects antero-lateral ambulacra immediately above petal, then extends anteriorly with a slight inward convexity along outside of coarse miliary band bounding anterior sulcus, to a point about midway from apical system to ambitus. Periproct dorsoventrally oval (Fig. 3); longer axis 12–20% TL, shorter axis 9–15% TL; posterior margin slopes anteriorly from keel to adoral surface. Sub-anal fasciole large, spectacle shaped (Fig. 4B), lateral margins incorporate 4–6 small pore pairs of posterior ambulacra Ia, Vb.

Plastron smooth, posterior portion finely granulated as are adjacent episternal plates, producing radiating semicircle just anterior of sub-anal fasciole. Peristome overhung by anteriorly projecting labrum resulting in slight lunate shape; broad (Fig. 5), width being 14–19% TL with length between 6–11% TL; surrounded by phyllode. Base shape controlled by nature of interambulacrum 5; generally bulbous to arched.

Distribution. *L. forbesii* is very common in the Mannum Formation in the River Murray cliffs at Mannum, South Australia, and is considered by Ludbrook (1969) to be Longfordian (Burdigalian) in age. Sadler et al. (1983) indicated the uncommon occurrence of *L. forbesii* in the overlying Morgan Limestone of Batesfordian (Langhian) age, but this occurrence requires conformation.
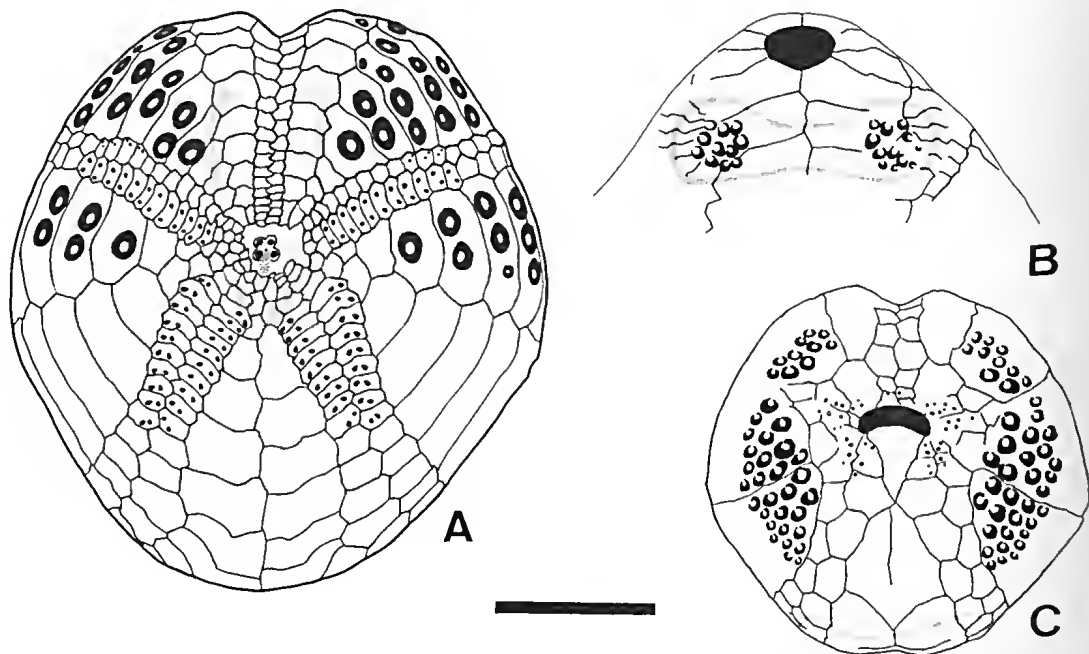
Fig. 4. *Lovenia woodsii* Etheridge. A, NMV P139210 adapical plating showing position of internal fasciole, pore pairs and distribution of primary tubercles. B, NMV P139210 posterior adoral surface indicating position of subanal fasciole. C, NMV P139211 adoral plating including phyllode. Scale bar represents 1 cm.

Fig. 5. Bivariate plot of peristome length expressed as a percentage of test length vs. test length indicating broad nature of *L. forbesii* (□) peristome compared to progressively narrower peristomes of *L. bagheerae* sp. nov. (○) and *L. woodsii* (+) respectively.

Lovenia woodsii (Etheridge 1875)

Figs 6, 7

Spatangus.—Forbes 1852: 50.

Spatangi.—Selwyn 1855: 5.

Hemipatagus Woodsii Etheridge 1875: 444–447, pl. 21, figs 1–7.—Woods 1878: 68.

Lovenia Forbesi, var. *minor* Duncan 1877: 44, 56–61, pl. 4, figs 5–8.—Etheridge 1878: 141.

Lovenia Forbesi, var. *Woodsi,* Etheridge. — Duncan 1877: 44, 56–61, pl. 4, figs 5–8.

Lovenia Forbesi, Woods & Duncan.— Duncan 1877: 44, 56–61, 63, pl. 4, figs 5–8.—Duncan 1887: 424–427.

Lovenia Forbesii, var. *Woodsii,* Etheridge.—Etheridge 1878: 141.

Lovenia Forbesii, Woods & Duncan.—Etheridge 1878: 141.

Lovenia Forbesi, McCoy.—McCoy 1879: 37–41, pl. 60, figs 1–4.

Lovenia Forbesi var. *Woodsii,* Etheridge.—Johnston 1887: 130.

Lovenia forbesi, Woods & Duncan.—Hall & Pritchard 1897: 191, 195.—Murray 1985: 190, pl. 7.9.23/A–C.

Lovenia forbesii, Woods & Duncan.—Hall & Pritchard 1897: 201, 202.

Lovenia forbesi, Woods.—Dennant & Kitson 1903: 132, 139.—Colliver 1937: 151, 153.—Singleton 1941: 33.—Kenley 1967: 38.

Lovenia woodsi, Etheridge. – Pritchard 1976 (1947): 20,
fig. 11. – Philip 1957: 403. – Carter 1963: 166, pl. 27,
fig. 9. – Philip 1963: 188. – Abele et al. 1976: 242. –
Holmes 1987: 33, fig. 4. – Abele et al. 1988: 316.
Lovenia forbesi. – Carroll 1949: 105. – David 1950: 528,
pl. 48e. – Rosengren 1988: 81, 83.
Lovenia forbesi var. *woodsi*, Etheridge. – Fletcher 1971:
134.
Lovenia. – Stone & Bawden 1975: 53, figured.
Lovenia woodsi. – Carter 1985: 17. – McNamara 1991b:
44.
Lovenia woodsii, Etheridge. – Archbold 1990: 119.

Lectotype. AM F17500, figured Etheridge (1875, pl. 21,
figs 1–7) and Fig. 6 herein, from the Late Miocene Black
Rock Sandstone, Beaumaris, on the east shore of Port
Phillip Bay, Victoria.

Material and locality. NMV P139210–P139219 from the
Cheltenhamian (Messinian) Black Rock Sandstone, Port
Phillip Basin, from the cliffs behind and immediately west
of Keefers Boatshed, 1.5 to 4 metres above sea level; NMV
P139220, 218 specimens from the same locality as above
(collected by N. W. Archbold).

Size ranges. Length 13.5–39.3 mm; width 13.1–37.3
mm; height 6.7–17.1 mm; width as % test length 88–
103%; (mean 94%); height as % test length 38–56%;
(mean 48%).

Diagnosis. Test diamond-shaped with maximum
width half-way. Deep anterior sulcus. Primary
tubercles few in number, restricted to anterior
half of test; rare in interambulacra 2a/3b. Antero-
lateral petals longer and narrower than posterior
petals, terminate ⅔ of distance to ambitus, conju-
gate pore pairs diverge toward apical system,
ambulacra IIb/IVa ¼–⅓ length of IIa/IVb. Peri-
proct compressed in dorso-ventral plane, peristome
antero-posteriorly narrow.

Description. Maximum test length of 40 mm;
widest about mid-test length, producing diamond
shaped test. Width varies between 88–103% TL.
Height varies between 38–56% TL. Distinct
anterior sulcus.

Apical system slightly anterior of mid-test length;
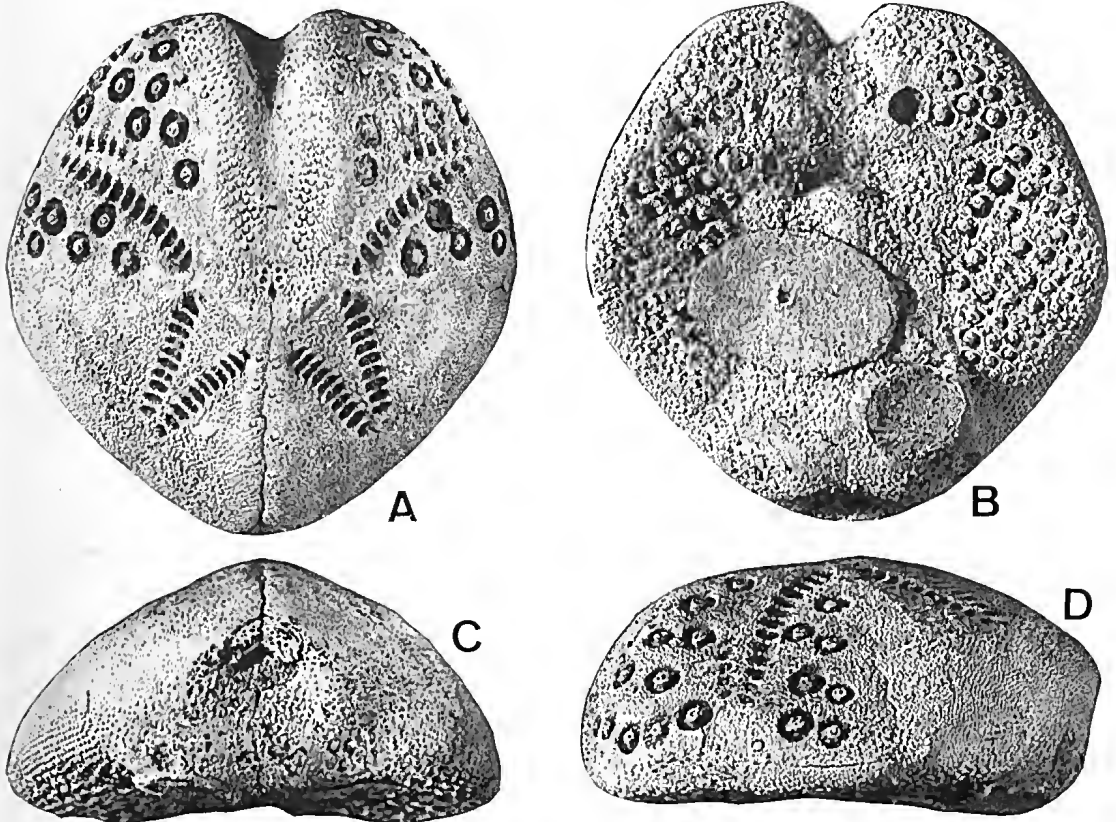
Fig. 6. A–D, *Lovenia woodsii* Etheridge. All figures ×2. A–D, AM F17500, holotype, adapical, adoral, posterior and lateral views.
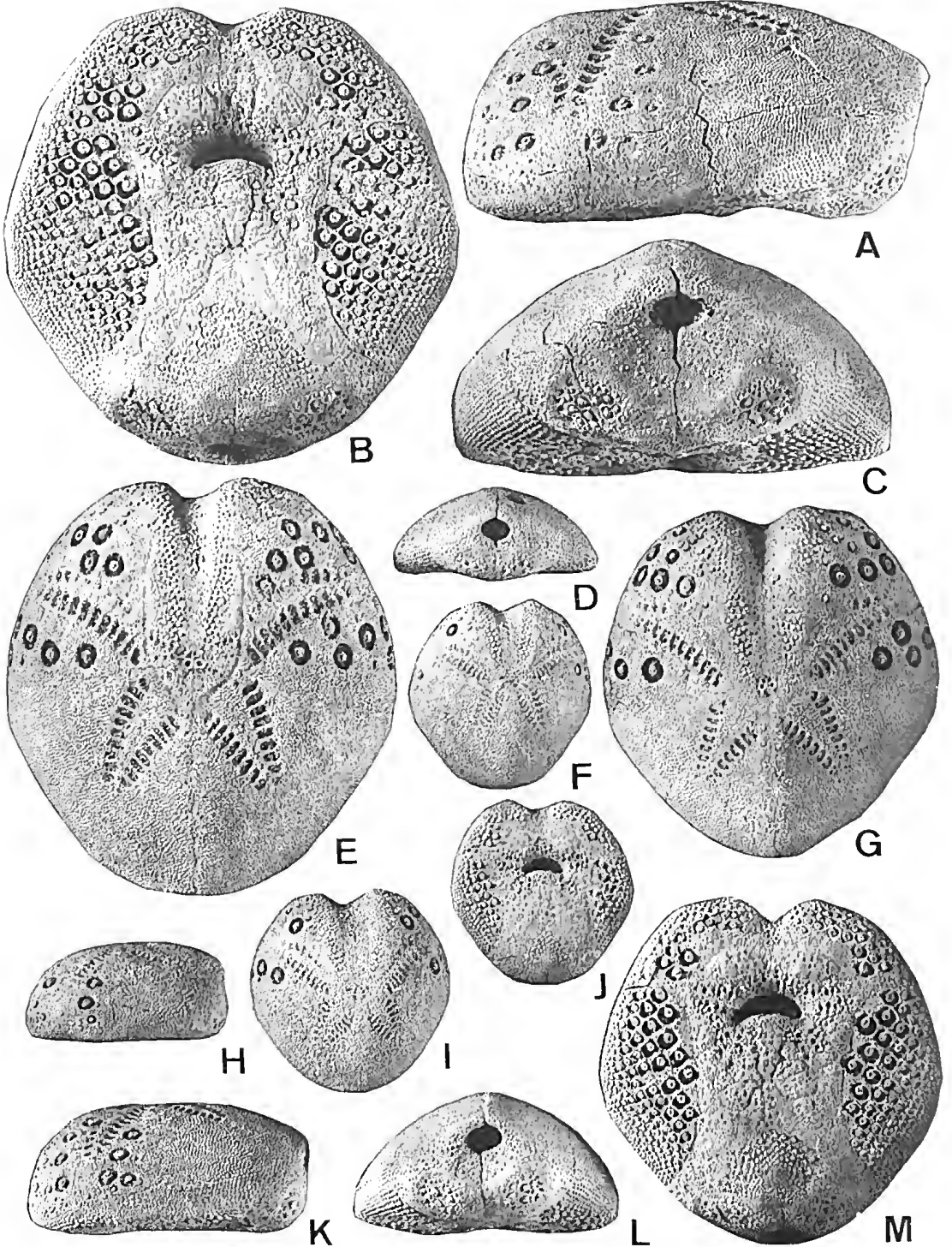
madreporite obovate, greatly separating posterior genital pores. Antero-lateral ambulacral petals terminate two-thirds distance to ambitus; anterior row of large pore pairs varies from ⅓–¼ posterior row length; conjugate pore apices linked by adapical ridge forming oval pit adorally. Ambulacra IIb, IVa small pore pairs diverge at about 90°, posterior rows diverge anteriorly at about 110°. 8–12 pore pairs in column IIa, mean 10.13; 9–13 in IVb, mean 10.68; 1–6 in IIb, mean 3.66; 1–6 in IVa, mean 3.60.

Posterior ambulacral petals wider than antero-lateral petals (Fig. 4A), both rows straight, equal in length; angle of divergence of anterior row about 50°, posterior row about 90°. Large pore pairs similar in size to antero-lateral petals; 6–11 pore pairs in column Ia, mean 8.4; 7–12 in Vb, mean 8.8; 6–10 in Ib, mean 7.8; 6–11 in Va, mean 8.1.

Primary tubercles absent from interambulacral columns Ia, 4b and 5a, b, rarely present in 2b and 3a, larger specimens exhibiting infrequent development; 0–2 primary tubercles in 2b, 3a, mean 0.1; 1 to 4 rows in columns 2a, 3b, 1 to 3 in Ib–4a; 2–11 primary tubercles in Ib, mean 4.9, 1–9 in 4a, mean 4.7; 2–14 in 2a, mean 6.6; 2–15 in 3b, mean 6.3. One aberrant specimen (NMV P139212) possessed one primary tubercle in interambulacrum 4b.

Periproct laterally elliptical (Fig. 3); longer axis 9–20% TL, shorter axis 7–14% TL; keel overhangs periproct producing concave posterior margin, termed beaked condition.

Peristome overhung by slightly bowed labrum, resulting in semi-circular to slight lunate shape (Fig. 4C); narrow (Fig. 5), length being 4–8% TL with width between 11–23% TL. Base shape generally flat to concave.

Remarks. This species has often been confused with *L. forbesii*, e.g. Singleton (1941), Kenley (1967) and Rosengren (1988). Hawkins (1916) reported on plate-crushing and resorption in the interambulacra of *L. forbesi* (*sic*) from no indicated locality, but as previously indicated by Philip (1957), the dimensions provided for the two specimens, 546A and 546B (housed in the University College, Reading, U.K.), suggest *L. woodsii*, as does Davies' (1935) figured *L. forbesi* (*sic*) from Victoria. However, accurate identification requires direct examination of the material.

Etheridge (1875) supplied four figures which closely approximated the species, but exaggerated

the number of pore pairs. Aslin (1980) reproduced those illustrations but further exaggerated those attributes which were erronous in the originals. Carter's (1963) topotype is a further example of an inaccurate illustration with pronounced asymmetry of the pore pairs, most of which exceed the observed range.

Pritchard (1976) provided an accurate series of diagrams in his fig. 11 of *L. woodsii*, as did Holmes (1987), fig. 4, with the exception of an abnormally high number of pore pairs in columns IIb and IVa.

Species differentiation. *L. woodsii* differs from *L. bagheerae* in its lower comparative number of adapical primary tubercles (Fig. 8), adapical divergence of the antero-lateral conjugate pore pairs and laterally elongated periproct (Fig. 3). Obvious in comparisons between populations is the antero-posteriorly narrow peristome (Fig. 5) and lesser number of pore pairs, apparent in ambulacra IIb (Fig. 9) of *L. woodsii*.

Distribution. *L. woodsii* is common at Beaumaris, being restricted to the Cheltenhamian (Messinian) Black Rock Sandstone of the Brighton
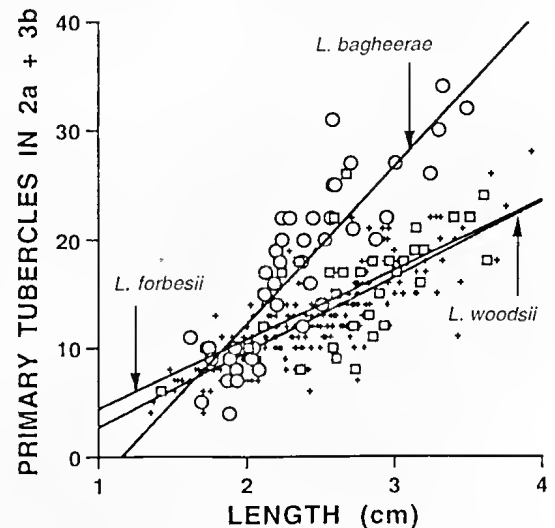
Fig. 8. Bivariate plot of combined number of primary tubercles in interambulacral columns 2a, 3b vs. test length showing increased attainment in *L. bagheerae* sp. nov. (○) as compared to *L. woodsii* (+) and *L. forbesii* (□).

Fig. 7. A–M, *Lovenia woodsii* Etheridge. All figures ×2. A–C, NMV P139213, lateral, adoral and posterior views; D, NMV P139218, posterior view; E, NMV P139214, adapical view, note internal fasciole; F, J, NMV P139219, adapical and adoral views; G, M, NMV P139215, adapical, and adoral views; H, I, NMV P139217, lateral and adapical views; K, L, NMV P139216, lateral and posterior views.

Group. Johnston (1877, 1888a, 1888b) reported *L. woodsii* from Table Cape, Tasmania, but it is likely that the species is either *L. forbesii* or an as yet undescribed phenotype.

Sadler et al. (1983) recorded *L. woodsii* from both the Morgan Limetone and Loxton Sands. If so the range of *L. woodsii* would span the Miocene and include the Pliocene as far as the Kalimnan (Zanclean).

Lovenia bagheerae Irwin sp. nov.

Fig. 10

Spatangus Forbesii. — Woods 1859: 91. — Woods 1862: 121.
Hemipatagus Forbesi, Woods & Duncan. — Woods 1865: 12.
Hemipatagus Forbesii, Woods & Duncan. — Woods 1865: 17, 19.
Lovenia Forbesii, Woods & Duncan. — Etheridge 1878: 141. — Woods 1878: 74.
Lovenia Forbesi, McCoy. — McCoy 1879: 37–40, pl. 60, figs 1–4.
Hemipatagus forbesii.–Dennant 1890: 445.

Fig. 9. Histogram of frequency of total number of pore pairs in ambulaeral column IIb for *L. woodsii* (△) and *L. bagheerae* sp. nov. (○) depicting similarly shaped but juxtaposed bell curves.

Lovenia forbesi, Woods. — Dennant & Mulder 1898: 86. — Dennant & Kitson 1903: 132.
Lovenia woodsi, Woods. — Chapman 1916: 401.
Lovenia woodsi, Etheridge. — Carter 1963: 166, pl. 27, figs 1, 2. — Abele et al. 1976: 214. — Abele et al. 1988: 288.
Lovenia woodsi. — Singleton 1968: 127. — Singleton 1973: 124.
Lovenia. — Mallett 1977: 79.

Etymology. Bagheera: P. Irwin's pet black cat (female), in loving memory of a very close friend.

Holotype. NMV P79247 from the early Late Miocene Mitchellian (Tortonian) Port Campbell Limestone, Portland, 300 km west of Melbourne, Victoria; F. A. Cudmore collection.

Paratypes. NMV P79233–P79270 including P78918, P78927, P78935, P78941, P78943 and P78953 from the same member/horizon and locality as the holotype.

Size ranges. Length 16.2–34.9 mm; width 5.9–32.6 mm; height 8.6–17.6 mm; width as % test length 88–99%; (mean 94%); Height as % test length 46–56%; (mean 51%).

Diagnosis. Test diamond-shaped with maximum width half-way. Deep anterior sulcus. High density of primary tubercles confined to anterior half of test; common in interambulacra 2a/3b. Anterolateral petals longer and narrower than posterior petals, terminate ⅔ of distance to ambitus, conjugate pore pairs do not diverge toward apical system, ambulacra IIb/IVa ⅓ length of IIa/IVb. Periproct almost circular, peristome antero-posteriorly broad.

Description. Test reaches a maximum known length of 35 mm; widest slightly posterior to mid-test length, producing diamond shaped test. Width varies between 88–99% TL. Height varies between 46–56% TL. Anterior sulcus pronounced. Apical system slightly posterior of mid-test length.

Posterior rows of antero-lateral petals diverge anteriorly at about 120°; anterior rows parallel posterior rows, barely diverging adapically; 9–14 pore pairs in column IIa, mean 10.4; 8–14 in IVb, mean 11.2; 3–7 in IIb, mean 4.6; 2–7 in IVa, mean 4.5.

Divergence of anterior row of posterior ambulacra about 45°, posterior row about 60°. 8–12 pore pairs in column Ia, mean 9.4; 8–12 in Vb, mean 9.6; 7–12 in Ib, mean 8.8; 7–11 in Va, mean 9.1.

Primary tubercles in 2b, 3a common for large specimens (Fig. 8), less frequent at smaller size;
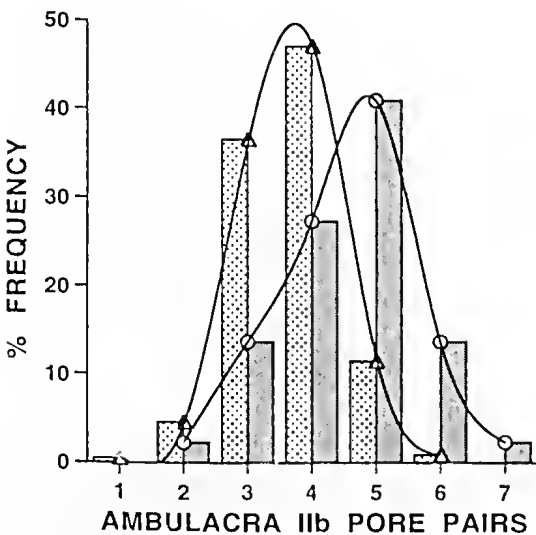
Fig. 10. A–L, *Lovenia bagheerae* sp. nov. All figures ×2. A, B, D, NMV P79263, paratype, lateral, adapical and posterior views; C, F, G, NMV P79254, paratype, lateral, adoral and posterior views; E, H, J, L, NMV P79247, holotype, adapical, adoral, posterior and lateral views; I, K, NMV P79248, paratype, adoral and adapical views.
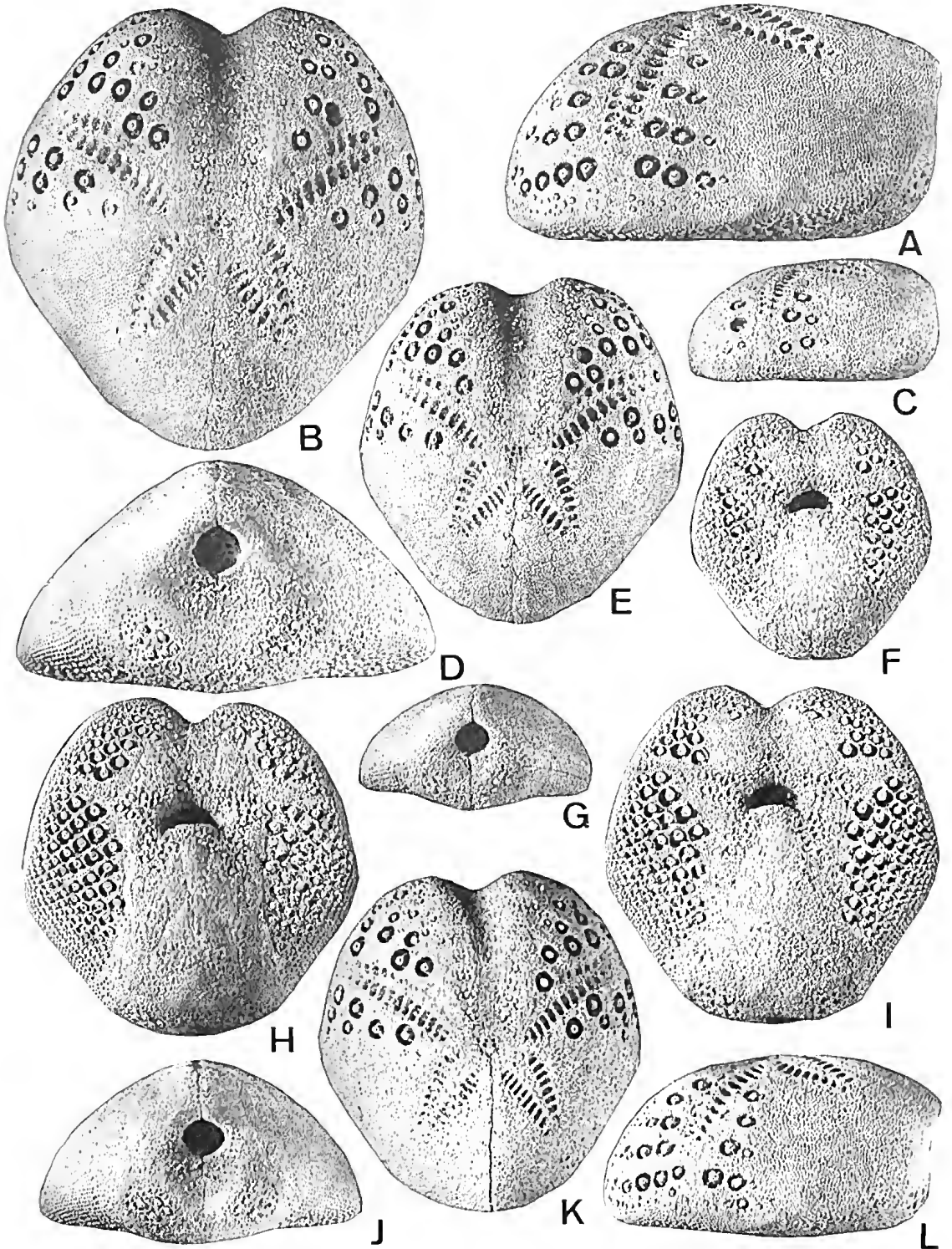
0–2 primary tubercles in 2b and 3a, mean 0.4; 1
to 5 rows in columns 2a–3b, 1 to 4 in 1b–4a; 1–11
primary tubercles in 1b, mean 5.9, 1–10 in 4a, mean
5.6; 1–18 in 2a, mean 9.0; 2–16 in 3b, mean 8.1.
Three aberrant specimens (NMV P79242, P79254,
P79262) possessed one primary tubercle in inter-
ambulacrum 1a or 4b.

Periproct obovate to rhomboidal (Fig. 3);
laterally 8–18% TL, dorso-ventrally 10–17% TL.
Sub-anal fasciole incorporates 3–5 small pore pairs
of ambulacra Ia, Vb.

Peristome length 4–11% TL, width 12–20% TL.
Base shape generally bulbous to arched.

Remarks. Woods (1859) was the first to observe
this species, classifying it with the Mount Gambier
taxon as *Spatangus Forbesii.* Duncan's fig. 3 (1864),
based on specimens from the Murray or Mount
Gambier was likewise considered to represent a *L.
forbesii* but is most representative of *L. bagheerae*
sp. nov. despite an exaggerated number of pore
pairs in the anterior rows of the anterior petals.
Etheridge (1878), McCoy (1879), Dennant (1890),
Dennant & Mulder (1898) and Dennant & Kitson
(1903) all assimilated the Portland population into
L. forbesii.

Chapman (1916), Singleton (1968, 1973) and
Abele et al. (1988) considered the population
at Portland to be *L. woodsi* (*sic*), as did Carter
(1963), figuring what could loosely be considered
L. bagheerae sp. nov. Mallett (1977) classified the
population to genus only.

McNamara (1987, 1989, 1990, 1991a) and
Holmes (1987) alluded to three Tertiary species of
Lovenia from south-east Australia, McNamara
(1991a) indicating the Peterborough Member of
the Port Campbell Limestone, this upper Middle
Miocene Member being found only in the Port
Campbell Embayment (Abele et al. 1988), Holmes
indicating an Early Pliocene age for a friable
limestone from Portland. The reported ages of
Middle Miocene and Early Pliocene for the un-
named species do not conform with the Late
Miocene Mitchellian (Tortonian) stage assigned to
that part of the Port Campbell Limestone which
is found to outcrop in the Portland cliffs (Singleton
et al. 1976) from which *L. bagheerae* sp. nov. is
derived.

Distribution. This new species has been described
solely from material collected from Portland,
Victoria. The specimens were removed from that
section of the Port Campbell Limestone repre-
senting the upper part of zone N16 and the basal
part of zone N17 (Singleton et al. 1976, Abele et al.
1988), making *L. bagheerae* sp. nov. Mitchellian
(Tortonian) in age.

If Duncan's fig. 3 (1864) of *L. woodsii* (*sic*),
reportedly from either the Murray River or Mount
Gambier is *L. bagheerae* sp. nov. then the time
range would extend to the Late Oligocene. Veri-
fication of temporal and spatial distributions is
required to resolve which species are present as
preliminary evidence points toward a larger number
of species than is currently known.

ONTOGENY

Investigation of the post-juvenile ontogenetic series
revealed considerable change in terms of size, shape
and number of the morphological features. Most
attributes exhibit allometric growth during develop-
ment with the resultant ontogenetic changes being:
a relative decrease in both the lateral and dorso-
ventral size of the periproct compared to the test
length; a relative decrease in the lateral and antero-
posterior (Fig. 5) size of the peristome relative
to the test length; a progressive increase in the
defensive adapical primary tubercles (Fig. 8) and
the lateral burrowing adoral primary tubercles;
an almost negligible increase in the number of
petaliferous pore pairs; a slight reduction in the
height and width of the test compared to test
length, except for *L. forbesii* which shows a minor
increase in both.

ACKNOWLEDGEMENTS

REFERENCES

Abele, C., 1988. Mesozoic and Cainozoic stratigraphy
of Victoria. In *Victorian Geology Excursion
Guide*, 1. Clark, B. Cook & G. C. Cochrane, eds,
Australian Academy of Science in conjunction
with the Geological Society of Australia (Victorian
Division), 39–46.

Abele, C., Gloe, C. S., Hocking, J. B., Holdgate, G.,
Kenley, P. R., Lawrence, C. R., Ripper, D.,
Threlfall, W. F. & Bolger, P. F., 1976.
Tertiary. In *Geology of Victoria*, J. G. Douglas
& J. A. Ferguson, eds, Geological Society of
Australia, Melbourne, Special Publication 5,
177–274.

Abele, C., Gloe, C. S., Hocking, J. B., Holdgate, G.,
Kenley, P. R., Lawrence, C. R., Ripper, D.,
Threlfall, W. F. & Bolger, P. F., 1988.

Tertiary. In *Geology of Victoria*, J. G. Douglas & J. A. Ferguson, eds, Victorian Division, Geological Society of Australia, Melbourne, 251–350.

ARCHBOLD, N. W., 1990. J. E. Tenison Woods: His contributions to the Tertiary geology of south eastern Australia. *Journal and Proceedings, Royal Society of New South Wales* 122: 119–121.

ASLIN, D., 1980. The *Lovenia* question—*forbesi* or *woodsi*. *The Fossil Collector* 2: 9–12.

BROWN, G. M. & STEPHENSON, A. E., 1991. Geology of the Murray Basin southeastern Australia. *Bureau of Mineral Resources, Geology & Geophysics, Bulletin* 235: 1–430.

BROWN, H. Y. L., 1910. Geology of the country south and east of the Murray River. In *South Australia Geological Reports and Explorations* 1889-1911, Government Printer, Adelaide, 1–7.

CARROLL, D., 1949. Mineralogy of the Cheltenhamian beds at Beaumaris, Victoria. *Journal of Sedimentary Petrology* 19: 104–111.

CARTER, A. N., 1963. The identity and age of the Portland *Lovenia*. In Boutakoff, N. A., The geology and geomorphology of the Portland area. *Memoirs of the Geological Survey of Victoria* 22: Appendix 4: 165–167.

CARTER, A. N., 1985. A model for depositional sequences in the Late Tertiary of southeastern Australia, In Stratigraphy, Palaeontology, Malacology: Papers in Honour of Dr Nell Ludbrook, J. M. Lindsay, ed., *Department of Mines and Energy, South Australia, Special publication* 5: 13–27.

CHAPMAN, F., 1914. *Australasian Fossils. A Student's Manual of Palaeontology*. George Robertson & Company, London, 341 p.

CHAPMAN, F., 1915. Report on a collection of fossils made by Dr A. Wade from the Cainozoic series of South Australia. In A. Wade, The supposed oil-bearing areas of South Australia. *Department of Mines. Geological Survey of South Australia. Bulletin* 4: Appendix 2: 44–50.

CHAPMAN, F., 1916. Cainozoic geology of the Mallee and other Victorian bores. *Department of Mines. Records of the Geological Survey of Victoria* 3: 327–430, pls 63–78.

CLAUS, C. F. W., 1876. *Grundzüge der Zoologie*. 3rd edn, Vol. 1. Marburg and Leipzig, 12 + 1254 p.

COLLIVER, F. S., 1937. Fossil localities in and about Melbourne Part II. Beaumaris. *Victorian Naturalist* 53: 151–153.

DARRAGH, T. A., 1985. Molluscan biogeography and biostratigraphy of the Tertiary of southeastern Australia. *Alcheringa* 9: 83–116.

DAVID, T. W. E., 1950. *The Geology of the Commonwealth of Australia*, W. R. Brown ed., Edward Arnold and Co., London, Volume 1, xx + 747 p., 58 pls, 28 tables.

DAVIES, A. M., 1935. *Tertiary Faunas—A Text Book for Oilfield Palaeontologists and Students of Geology, vol. 1—The Composition of Tertiary Faunas 1st edn*, Thomas Murby & Co., London, xi + 406 p.

DENNANT, J., 1890. Observations on the Tertiary and post-Tertiary geology of southwestern Victoria. In *Report of the second meeting of the Australasian Association for the Advancement of Science held at Melbourne, Victoria, in January, 1890*, W. B. Spencer, ed., Ford and Son, Melbourne, 441–452.

DENNANT, J. & KITSON, A. E., 1903. Catalogue of the described species of fossils (except Bryozoa and Foraminifera) in the Cainozoic fauna of Victoria, South Australia and Tasmania. *Department of Mines. Records of the Geological Survey of Victoria* 1: 89–147.

DENNANT, J. & MULDER, J. F., 1898. The geology of the Lower Leigh Valley. *Proceedings of the Royal Society of Victoria* 11: 54–95, pls 5–6.

DESOR, E., 1847. *Synopsis des Échinides Fossiles*. C. Reinwald, ed., Paris, 490 p., 44 pls.

DUNCAN, P. M., 1864. A Description of some fossil corals and echinoderms from the South-Australian Tertiaries. *The Annals and Magazine of Natural History* 14: 161–168, pls 5–6.

DUNCAN, P. M., 1870. On the fossil corals (Madreporaria) of the Australian Tertiary deposits. *Quarterly Journal of the Geological Society, London* 26: 284–318, pls 19–22.

DUNCAN, P. M., 1877. On the Echinodermata of the Australian Cainozoic (Tertiary) deposits. *Quarterly Journal of the Geological Society, London* 33: 42–73, pls 3–4.

DUNCAN, P. M., 1887. A revision of the Echinoidea from the Australian Tertiaries. *Quarterly Journal of the Geological Society, London* 43: 411–430.

ETHERIDGE, R., 1875. Description of a new species of the genus *Hemipatagus*, Desor, from the Tertiary rocks of Victoria, Australia, with notes on some previously described species from South Australia. *Quarterly Journal of the Geological Society, London* 31: 444–450, pl. 21.

ETHERIDGE, R., 1978. *A Catalogue of Australian Fossils (Including Tasmania and the Island of Timor) Stratigraphically and Zoologically Arranged*. Cambridge University Press, 232 p.

FISCHER, A. G., 1966. Spatangoids. In *Treatise on Invertebrate Paleontology. Part U. Echinodermata 3(2)*, R. C. Moore, ed., Geological Society of America and University of Kansas Press, Lawrence, 543–628.

FLETCHER, H. O., 1971. Catalogue of type specimens in the Australian Museum, Sydney. *Australian Museum, Sydney, Memoir* 3: 1–167.

FORBES, E., 1852. Our knowledge of Australian rocks as derived from their organic remains. In *Lectures on Gold for the Instruction of Emigrants About to Proceed to Australia*, J. B. Jukes *et al.*, David Bogue, London, 41–67.

GRAY, J. E., 1845. In Eyre. Journal of Expedition of Discovery into Central Australia. 1. p. 436, pl. 6(2).

HALL, T. S. & PRITCHARD, G. B., 1897. A contribution to our knowledge of the Tertiaries in the neighbourhood of Melbourne. *Proceedings of the Royal Society of Victoria* 9: 187–229.

HAWKINS, H. L., 1916. A remarkable structure in *Lovenia Forbesi* from the Miocene of Australia. *Geological Magazine* 53: 100-105, pl. 6.

HOLMES, F., 1987. A brief review of Australian Tertiary echinoids. *The Fossil Collector* 22/23: 25-36.

HOWCHIN, W., 1928. *The Building of Australia and the Succession of Life: With Special Reference to South Australia. Part 2. Mesozoic and Cainozoic.* Government Printer, Adelaide, 243 p.

JOHNSTON, R. M., 1877. Further notes on the Tertiary marine beds of Table Cape, Tasmania. *Papers and Proceedings and Report of the Royal Society of Tasmania* for 1876: 79-116.

JOHNSTON, R. M., 1887. Reference list of the Tertiary fossils of Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* for 1886: 124-140.

JOHNSTON, R. M., 1888a. *Systematic Account of the Geology of Tasmania.* Government Printer, Hobart, 408 p.

JOHNSTON, R. M., 1888b. Observations with respect to the nature and classification of the Tertiary rocks of Australasia. *Papers and Proceedings of the Royal Society of Tasmania* for 1887: 135-207.

KENLEY, P. R., 1967. Geology of the Melbourne district – Tertiary. *Bulletin of the Geological Survey of Victoria* 59: 30-46.

LAMBERT, J., 1905. Échinides du sud de la Tunisie (environs de Tatahouine). *Société géologique de France. Bulletin* Ser. 4, 5: 569-577, pl. 22.

LAUBE, G. C., 1869. Uber einige fossile Echiniden von den Murray cliffs in Sud-Australien. *Sitzungberichte der mathematisch-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften zu Wien* 59: 183-198, + plate.

LESKE, N. G., 1778. *Jacobi Theodori Klein naturalis dispositio echinodermatum ..., edita et descriptionibus novisque inventis et synonomis auctorem aucta.* Leipzig, 278 p., 54 pls.

LUDBROOK, N. H., 1957. A reference column for the Tertiary sediments of the South Australian portion of the Murray Basin. *Journal and Proceedings of the Royal Society of New South Wales* 90: 174-180.

LUDBROOK, N. H., 1958. The Murray Basin in South Australia. In The geology of South Australia prepared by members of the South Australian Division of the Geological Society of Australia, M. F. Glaessner & L. W. Parkin, eds. *Journal of the Geological Society of Australia* 5: 102-114, fig. 21.

LUDBROOK, N. H., 1961. Stratigraphy of the Murray Basin in South Australia. *Department of Mines. Geological Survey of South Australia.* Bulletin 36: 96 p. + 8 pls.

LUDBROOK, N. H., 1969. Tertiary Period. In *Handbook of South Australian Geology*, L. W. Parkin, ed., Government Printer, Adelaide, 172-203.

MALLETT, C. W., 1977. *Studies in Victorian Tertiary foraminifera: Neogene planktonic faunas.* Ph.D. thesis, University of Melbourne (Unpub.). Part 1, 265 p.

MALLETT, C. W. & HOLDGATE, G. R., 1985. Subsurface Neogene stratigraphy of Nepean Peninsula, Victoria. In Stratigraphy, palaeontology, malacology: papers in honour of Dr Nell Ludbrook, J. M. Lindsay, ed. *Department of Mines and Energy, South Australia, Special publication* 5: 233-245.

McCOY, F., 1879. Tertiary Echinodermata. In *Prodromus of the Palaeontology of Victoria or Figures and Descriptions of the Victorian Organic Remains, Decade VI.* Geological Survey of Victoria, Melbourne, 33-44.

McNAMARA, K. J., 1987. Plate translocation in spatangoid echinoids: its morphological, functional and phylogenetic significance. *Paleobiology* 13: 312-325.

McNAMARA, K. J., 1989. The role of heterochrony in the evolution of spatangoid echinoids. *Geobios*, mémoire spécial 12: 283-295.

McNAMARA, K. J., 1990. Echinoids. In *Evolutionary Trends*, K. J. McNamara, ed., Bellhaven Press, London, 205-231.

McNAMARA, K. J., 1991a. A guide to the echinoids of the Middle Miocene Rutledge Marl, Victoria. *The Victorian Naturalist* 108: 8-19.

McNAMARA, K. J., 1991b. Murder and Mayhem in the Miocene: A spine chilling tale of sea urchin slaughter. *Natural History* 8/91: 40-47.

McNAMARA, K. J. & AH YEE, C., 1989. A new genus of brissid echinoid from the Miocene of Australia. *Geological Magazine* 126: 177-186.

MELVILLE, R. V. & DURHAM, J. W., 1966. Skeletal morphology. In *Treatise on Invertebrate Paleontology. Part U. Echinodermata 3(2)*, R. C. Moore, ed., Geological Society of America and University of Kansas Press, Lawrence, 220-257.

MURRAY, J. W., 1985. Class Echinoidea (Ordovician-Recent). In *Atlas of Invertebrate Macrofossils*, J. W. Murray, ed., Longman Group Limited and The Palaeontological Association, London, 182-190.

PHILIP, G. M., 1957. Interambulacral plate atrophy in *Lovenia woodsi*. *Geological Magazine* 94: 402-408.

PHILIP, G. M., 1963. The Tertiary echinoids of southeastern Australia. I. Introduction and Cidaridae (1). *Proceedings of the Royal Society of Victoria* 76: 181-226, pls 21-26.

PRITCHARD, G. B., 1892. Catalogue of Australian older Tertiary Mollusca and Pliocene species in South Australian School of Mines Museum. *The Annual Report of the South Australian School of Mines and Industries and Technological Museum* for 1891: 176-206.

PRITCHARD, G. B., 1976. Geology of the Sandringham-Beaumaris coastline. *The Victorian Naturalist* 93: 4-20.

ROSENGREN, N. J., 1988. *Sites of Geological and Geomorphological Significance on the Coast of Port Phillip Bay, Victoria.* Ministry for Planning and Environment, Victoria, 268 p.

SADLER, T., PLEDGE, N. S. & MORRIS, R., 1983. *Fossils*

of Southern Australia Part 1: Sea Urchins of the Murray River Cliffs. Quoll Enterprises, Seaton, South Australia, 33 p.

SELWYN, A. R. C., 1855. On the geology, palaeontology and mineralogy of the country between Melbourne, Western Port Bay, Cape Schanck and Point Nepean. In Geological Surveyor's Report. In *Votes and Proceedings of the Legislative Council* 1: 1–10.

SINGLETON, F. A., 1941. The Tertiary geology of Australia. *Proceedings of the Royal Society of Victoria* 53: 1–125.

SINGLETON, O. P., 1968. Otway region. In *A Regional Guide to Victorian Geology 1st edn*, J. McAndrew & M. A. H. Marsden, eds, Geology Department, University of Melbourne, 117–131 + fig.

SINGLETON, O. P., 1973. Mesozoic and Tertiary stratigraphy of the Otway region. In *Regional Guide to Victorian Geology 2nd edn*, J. McAndrew & M. A. H. Marsden, eds, School of Geology, University of Melbourne, 114–128 + fig.

SINGLETON, O. P., McDOUGALL, I. & MALLETT, C. W., 1976. The Pliocene–Pleistocene boundary in southeastern Australia. *Journal of the Geological Society of Australia* 23: 299–311.

STONE, D. M. & BAWDEN, S. N., 1975. *Australian Fossils*. Golden Press, Sydney, 111 p.

STURT, C., 1833. *Two Expeditions into the Interior of South Australia During the Years 1828, 1829, 1830, and 1831: with Observations on the Soil, Climate, and General Resources of the Colony of New South Wales. Volume II*. Smith, Elder and Co., Cornhill, London, 271 p.

TATE, R., 1885. Notes on the physical and geological features of the basin of the lower Murray River.

Transactions and Proceedings and Report of the Royal Society of South Australia 7: 24–46, pl. 3.

TATE, R. & DENNANT, J., 1893. Correlation of the marine Tertiaries of Australia. Part I., Victoria, with special notes on the Eocene beds at Spring Creek and at the mouth of the Gellibrand River. *Transactions of the Royal Society of South Australia* 17: 203–226, pls 1–2.

TRUSWELL, E. M., CHAPRONIERE, G. C. H. & SHAFIK, S., 1991. Australian Phanerozoic Timescales 10. Cainozoic. *Bureau of Mineral Resources, Geology and Geophysics*, Record 1989/40: 1–16.

WOODS, J. E. T., 1859. Remarks on a Tertiary deposit in South Australia. *Transactions of the Philosophical Institute of Victoria* 3: 85–94.

WOODS, J. E. T., 1860. On some Tertiary rocks in the colony of South Australia. *The Quarterly Journal of the Geological Society of London* 16: 253–261.

WOODS, J. E. T., 1862. *Geological Observations in South Australia, Principally in the District South-East of Adelaide*. Longman, Green, Longman, Roberts and Green, London, xviii + 404 p.

WOODS, J. E. T., 1865. *The Geology of Portland: Two lectures Delivered in Portland, Feb. 10th and 13th 1865*. W. Cooper, Guardian Office, Portland, 19 p.

WOODS, J. E. T., 1867a. The Tertiary rocks of South Australia. No. 1. — Introduction. *Papers of the Adelaide Philosophical Society* for 1865–1866: 3 p.

WOODS, J. E. T., 1867b. The Tertiary rocks of South Australia. Pt IV. — Fossil Echinidae. *Papers of the Adelaide Philosophical Society* for 1865–1866: 2 p., pl. 3.

WOODS, J. E. T., 1878. On the Tertiary deposits of Australia. *Journal of the Royal Society of New South Wales* 11: 65–79.

ORIGINS AND DISPERSAL OF A BRACHIOPOD FAMILY—THE SYSTEMATICS, BIOGEOGRAPHY AND EVOLUTION OF THE FAMILY TEREBRATELLIDAE

J. R. RICHARDSON

Museum of Victoria, 328 Swanston Street, Melbourne, Victoria 3000

RICHARDSON, J. R., 1994:12:31. Origins and dispersal of a brachiopod family—the systematics, biogeography and evolution of the Family Terebratellidae. *Proceedings of the Royal Society of Victoria* 106: 17–29. ISSN 0035-9211.

Three southern subfamilies of the Terebratellidae (Bouchardiinae, Anakineticinae, Terebratellinae) are redefined using cardinal process shape and presence or absence of some components of the cardinalia (crural bases, hinge plates). The subfamilies are confined to the seas around Gondwana-derived land masses between Antarctic shorelines and latitudes of approximately 30°S and, with the exception of 2 Late Cretaceous genera, to the Cainozoic era. Species without adaptations for particular substrates in Antarctica, the subantarctic islands, Australia, New Zealand and South America show certain similarities suggesting that they were derived by vicariance from generalist stocks which occupied some sections of the shorelines and shelf of Gondwana. This record of the Terebratellidae does not conform with the only current model for brachiopod distribution (Zezina 1985)—that seas in low latitudes have provided both a cradle and refuge for inarticulates and articulates.

THE PHYLUM Brachiopoda provides a record of life on earth that is remarkable in the history of its 2 divisions, one of which (Inarticulata) is static, the other (Articulata) repetitive (Cooper 1970; Rudwick 1970). Despite the excellence (in length, continuity and abundance) and clarity of the record, studies have yielded little information on the processes of macroevolution or on the nature of relationships within the phylum. Difficulties in utilising the record can be attributed in large part to the lack of knowledge of the variability of living populations and so of the nature of relationships between species—one consequence of the inaccessibility of living species in many parts of the world. For example, New Zealand is the only country known in which species of polytypic genera are known to be accessible to direct study.

During the last 2 decades studies of the members of one family, the Terebratellidae, have given greater biological understanding of articulate brachiopods. This family provides more information than others because it is the only one in which living outnumber fossil genera and because of the abundance of its members in the Southern Hemisphere. In the Ross Sea, for example, Foster (1974, 1989) has observed that brachiopods outnumber bivalve molluscs. They are common to abundant in the Magellanic province of South America (McCammon 1973; Cooper 1973), the subantarctic waters of the Atlantic (Cooper 1982) and Indian (Cooper 1981) oceans and in the sands of the shelf of southern Australia (Richardson 1987). In New Zealand they are dominant members of the benthos of many southern inlets and of all the fiords (Richardson 1981a).

The abundance of living members of the family in these areas has provided information on the variability of populations in most parts of its range and on factors that govern distribution. In addition many species are sufficiently accessible for the direct study of substrate relationships and behaviour. These studies of the living together with the rich Tertiary faunas of Australia and New Zealand mean that sufficient data are now available about the members of one family to enable speculation on the centres of origin of species, on paths and rates of dispersal, and on relationships among genera.

SYSTEMATICS

Superfamily **Terebratelloidea** King, 1850

Family **Terebratellidae** King, 1850

Diagnosis. Non-strophic Terebratellacea without spicules and dental plates and in which lateral connecting bands are formed during development of the loop. Upper Cretaceous to Recent.

Subfamily **Bouchardiinae** Allan 1940

Diagnosis. Sulcate, posteriorly thickened smooth Terebratellidae with a hypothyrid or epithyrid foramen, and with cardinalia consisting of socket ridges and a cardinal process with a bilobed posterior surface.

Genera included. *Bouchardia* Davidson, 1850; *Bouchardiella* Doello-Jurado, 1922; *Malleia* Thomson, 1927; *Neobouchardia* Thomson, 1927.

Distribution.   Cretaceous–Recent; Australia, New Zealand, Antarctica, South America.

Subfamily **Anakineticinae** Richardson 1991

Diagnosis.   Rectimarginate to sulcate, posteriorly thickened, smooth Terebratellidae with permeso-thyrid foramen, cardinalia consisting of socket ridges, crural bases and a cardinal process with trifid posterior surface.

Genera included.   *Anakinetica* Richardson, 1987; *Adnatida* Richardson, 1991; *Aliquantula* Richardson, 1991; *Australiarcula* Elliott, 1959; *Elderra* Richardson, 1991; *Magadina* Thomson, 1915; *Magadinella* Thomson, 1915; *Parakinetica* Richardson, 1987; *Pilkena* Richardson, 1991; *Pirothyris* Thomson, 1927; *Rhizothyris* Thomson, 1915.

Distribution.   Cretaceous–Recent; Australia, New Zealand.

Subfamily **Terebratellinae** King 1850

Diagnosis.   Rectimarginate to sulcate to intra-plicate, smooth or costate Terebratellidae with cardinalia consisting of socket ridges, crural bases, hinge plates and a transverse cardinal process, posterior thickening present or absent.

Genera included.   *Aerothyris* Allan, 1939; *Aneboconcha* Cooper, 1973; *Austrothyris* Allan, 1939; *Calloria* Cooper & Lee 1993; Allan, 1939; *Diedrothyris* Richardson, 1980; *Dyscritosia* Cooper, 1982; *Fosteria* Zezina, 1980; *Gyrothyris* Thomson, 1918; *Jaffaia* Thomson, 1927; *Magasella* Dall, 1870; *Magella* Thomson, 1915; *Magellania* Bayle, 1880; *Neothyris* Douvillé, 1879; *Pachymagas* Ihering, 1903; *Stethothyris* Thomson, 1918; *Syntomaria* Cooper, 1982; *Terebratella* d'Orbigny, 1846; *Victorithyris* Allan 1940; *Waiparia* Thomson 1920.

Distribution.   Upper Cretaceous–Recent. Southern Hemisphere between Antarctic shelf and latitudes of approximately 35°.

Comments.   Foster (1974), in a comprehensive study of Recent terebratellid species from the Southern Hemisphere, differentiated genera within the Terebratellidae on loop form. He stated that use of the loop seemed artificial but that it was the simplest means of classification in such a large group with 'the limited number of morphological features of apparent taxonomic value, the high degree of variability within individual species, the great amount of apparent convergence, and the poorly known fossil record' (1974, p. 97).

Work on Australian Tertiary Terebratellidae (Richardson 1973, 1980, 1991) has clarified relationships within the family to some extent in that three of the subfamilies (Bouchardiinae, Anakineticinae, Terebratellinae) can now be defined with greater precision using components that make up the cardinalia. The subfamily Neothyrinae is not retained because both Foster (1974) and Richardson (1975, 1980) have shown that the characters used by Allan (1940) to distinguish members of the subfamily (bifurcated septum and a hinge trough) are a consequence of the differential thickening of inner hinge plates; i.e. the Neothyrinae was erected for genera that differ from those included in the Terebratellinae only in degrees of calcification (Figs 1, 2).

The other subfamily (Trigonoseminae) referred to the Terebratellidae by Elliott (1965) includes three genera from Upper Cretaceous deposits in Europe, North America and Western Asia. Loop characters indicate that it should be assigned to the Terebratellidae but the nature of its relationship to southern subfamilies is difficult to determine without study of the cardinalia of juvenile specimens. Descriptions of the genera included in the
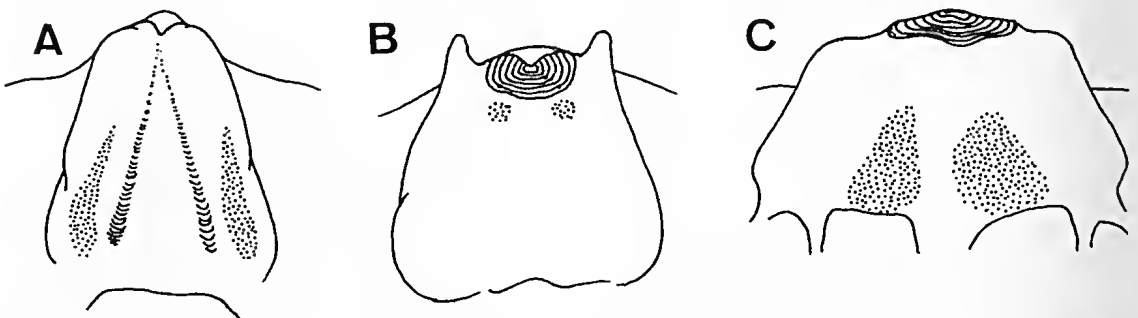
Fig. 1.   Outline drawings of the cardinalia to show areas of attachment of the diductor and dorsal adjustor muscles in representative adults of the 3 terebratellid subfamilies — Bouchardiinae (*Bouchardia rosea*), Anakineticinae (*Anakinetica cumingi*), Terebratellinae (*Magasella sanguinea*).

Trigonoseminae indicate that, like the Anakineticinae and free-living Bouchardiinae, the cardinalia are thickened and without hinge plates but otherwise they do not resemble any southern taxa. Furthermore, neither cardinalia nor the cardinal process appear to be consistent in form within the subfamily.

In the classification proposed herein, precedence is given to those characters associated with the substrate relationships of a species for 3 reasons:

1. Variability of the pedicle system. The pedicle system may vary intra- and interspecifically and within and between all higher taxa (Richardson 1981) whereas other soft parts (gut form, numbers of coelomoducts) may differ between orders but appear to be consistent in form and function in the members of each order.

2. Functional morphology. Features of the shell used in classification are directly related to differences in the pedicle system and therefore to substrate relationships. They are:

the beak and cardinalia that house and therefore reflect any differences in the pedicle system, e.g. the area of attachment of the dorsal adjustor muscles differentiates forms with a free or bonded pedicle (Figs 1, 2, 3);

the size of the cardinal process which is determined by the area of attachment required by the diductor muscles. The size of the process in free forms indicates that greater leverage is needed to open the shell in free than in fixed forms; and

differential thickening which is found in free forms only and is the means by which the shell is stabilised and oriented.

3. Species of polytypic genera and populations of species studied show that they are differentiated on characters reflecting differences in substrate relationships, e.g. the free and sedentary populations of *Calloria inconspicua* and of *Magasella sanguinea* (Aldridge 1981; Stewart 1981) and species of *Neothyris* (Aldridge 1991).

Some families of the Terebratellidae (Laqueidae, Dallinidae, Terebratellidae) are differentiated on the nature of loop development but the stage of development does not define lower categories. Adult loop patterns within a family appear to be correlated with the amount of space available within the mantle cavity since no species with a large mantle cavity is known with an axial loop and no species with a small mantle cavity is known with a teloform loop. From studies of Mesozoic Terebratelloidea, Owen (1977) has also stressed the importance of the cardinalia in defining taxa at subfamily levels.

The cardinalia and classification. Figs 1–3 illustrate differences in the cardinalia that distinguish the 3 southern subfamilies. They differ in cardinal process shape (bilobed, trifid, transverse), in the presence or absence of hinge plates and in the areas used for the attachment of the dorsal adjustor muscles. In the Terebratellinae these muscles are attached anterior to the cardinal process and to hinge plates which occupy the area bounded by the socket ridges. In the Anakineticinae and Bouchardiinae the muscles are attached to respectively pits and furrows that flank the cardinal process. The pits of the Anakineticinae are confined to the posterior part of the platform, the furrows of the Bouchardiinae extend the length of the platform. Differences in function associated with the position of attachment of the muscles are described under substrate relationships. The absence of crural bases in the Bouchardiinae is linked to the absence of descending branches of the loop which consists of a ring supported by a high median septum.

The hinge plates that characterise the Terebratellinae occupy the area bounded by the socket ridges. Hinge plates also differentiate genera within the subfamily according to their relationship with crural bases, socket ridges, median septum, and whether they are lamellar or solid, excavate or sessile i.e., adpressed to the valve floor.

The common pattern of the cardinalia in living terebratellinids is one in which the socket ridges and crural bases are fused or confluent or are narrowly separated by outer hinge plates with inner hinge plates meeting on the septum. In these species the crural bases are traces of the crura. In two Recent species, *Magellania joubini* and *Magellania fragilis*, the crural bases separate inner and outer hinge plates which are roughly equal in width. In this character, the hinge plates are similar to those in the Tertiary genera, *Diedrothyris* and *Stethothyris*. The crural bases of *Austrothyris* and *Cudmorella* (Fig. 3C) differ from those of all other genera in that they are prominent structures with sharp ridges which, in ventral view, project above the level of the hinge plates. In these genera also the inner hinge plates are adpressed to the valve floor and extend onto the median septum for approximately half its length. Foster (1974) has noted that the hinge plates of *Aerothyris kerguelensis* vary in position, most are sessile, others are excavate. The significance of differences in the position and prominence of crural bases and in the angle at which hinge plates lie relative to the valve floor and septum is unknown. Richardson & Mineur (1981) compared the hinge plates of *Magasella sanguinea* with those of *Calloria inconspicua* and concluded that the greater elevation of

the plates of the former species was related directly to the line of action of the dorsal adjustor muscles and indirectly to shell curvature and to beak and pedicle size. Analyses of hinge plate condition in relation to the functioning of the dorsal adjustor muscles in other species would be a productive study.

The cardinal process of the Bouchardiinae is bilobed with the posterior striated surface extending as an inverted V from the posterior tip of the dorsal valve. Differences in the extent of the lobes in different genera are presumably associated with life style. *Bouchardia* is a free living form with a free pedicle which probably functions in similar
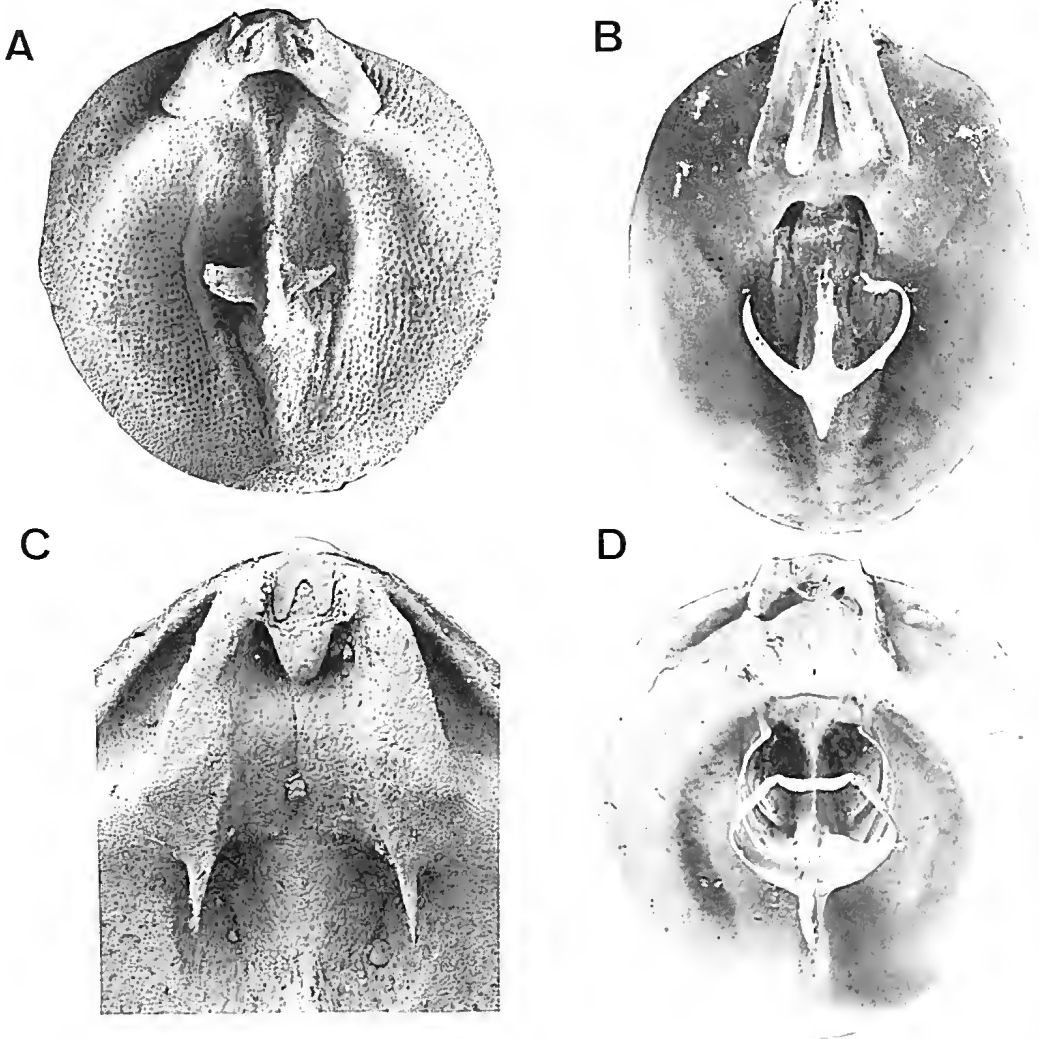
Fig. 2. Dorsal valve interiors of species from the subfamilies Bouchardiinae and Anakineticinae which show differences in the cardinal process and in the areas used for attachment of the dorsal adjustor muscles. A, B, *Malleia portlandica* (×12) and *Bouchardia rosea* (×5) (Bouchardiinae) with bilobed cardinal processes and with areas of attachment of the dorsal adjustor muscles lying between the socket ridges and the cardinal process. C, D, *Anakinetica cumingi* (Anakineticinae), young (×30) and adult (×5) specimens with trifid cardinal processes and attachment for the dorsal adjustor muscles at the antero-lateral corners of the posterior surface of the cardinal process.

ratchet-like fashion to that of *Anakinetica*. *Malleia* (Tertiary) was probably sedentary in habit in that its small size and beak, plano-convex shape and hypothyrid foramen are features associated with fixed forms in modern seas.

The striated posterior surface of the cardinal process of the Anakineticinae is trifid, i.e. it con-

sists of three surfaces approximately equal in size, two lateral surfaces flanking one ventrally facing median surface.

The cardinal process of most of the species included in the Terebratellinae is transverse with a median notch at the junction of the striated posterior and smooth anterior surfaces. The car-
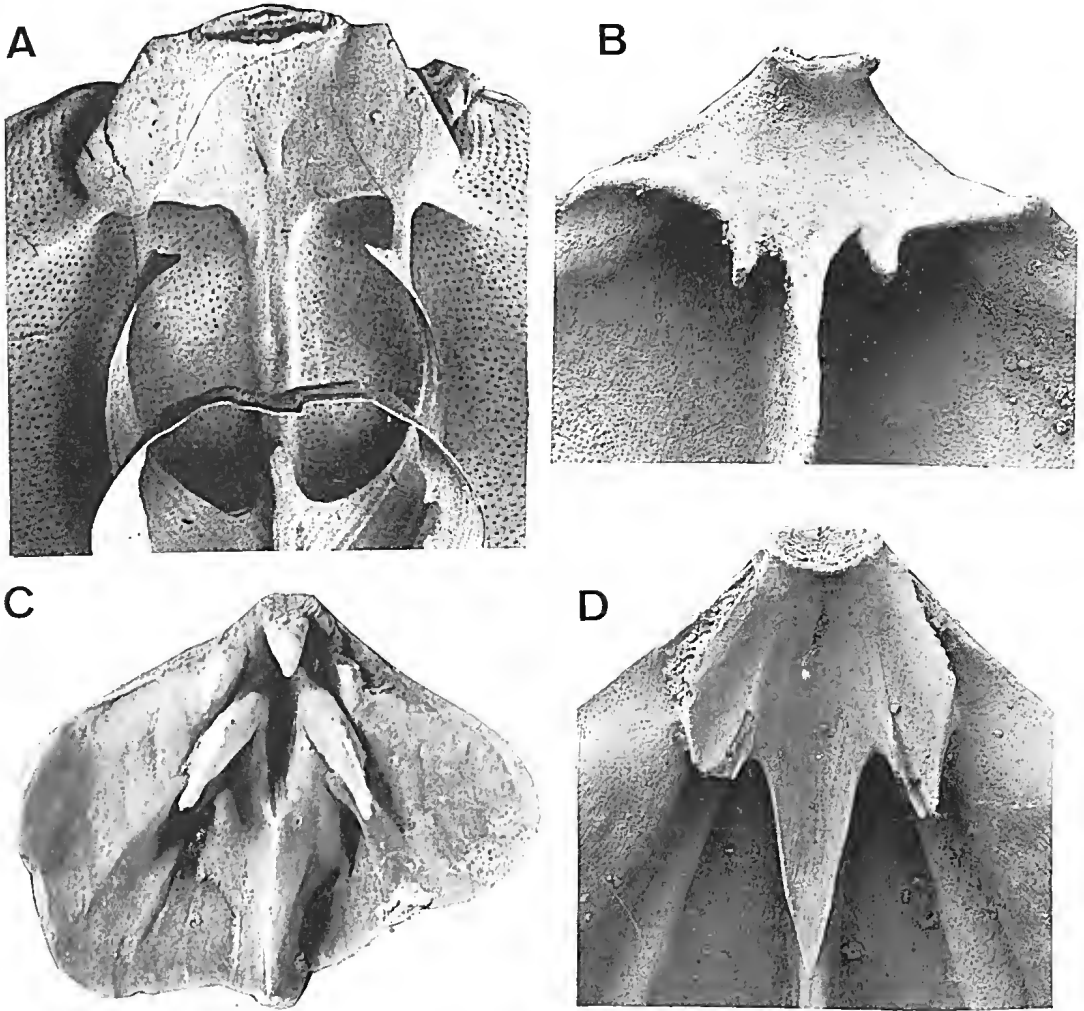
Fig. 3. Dorsal valve interiors of species of terebratellinae genera which illustrate cardinal process shape (transverse), differences in the disposition of hinge plates which provide areas of attachment of the dorsal adjustor muscles, and the effects of differential thickening on the appearance of the cardinalia. A, *Neothyris lenticularis* juvenile (×30). B, *Stethothyris pectoralis* (×6) juvenile in which crural bases separate inner and outer hinge plates. C, *Cudmorella corioensis* (×3) juvenile in which crural bases with sharp ridges project above the level of the hinge plates and in which inner hinge plates extend anteriorly onto the septum. D, *Cudmorella corioensis* adult (×1.5) in which differential thickening gives a superficial appearance of bifurcation of the septum.

dinal processes of young specimens of *Anakinetica cunningi* and *Neothyris lenticularis* (Figs 2C, 3A) show the differences in shape characteristics of the two subfamilies. In terebratelline species with differential thickening, the anterior surface of the cardinal process is large and may be globose or columnar in outline. *Neothyris lenticularis*, in particular, shows great variability in the shape of the process and, as noted by Foster (1974), specimens may display lateral flanges with strong inwards curvature and a trefoil posterior surface. Similar convergent trends have been described by Cooper for the Productacea 'Each of the major families of the Productacea has its own type of cardinal process, characteristic of the family as shown by young or young adults but in old age all tend toward a common trilobed cardinal process' (1969, p. 229).

Morphological variability. The genera included in the Bouchardiinae and Anakineticinae can be clearly defined but the variability of species within the Terebratellinae make generic separation difficult as noted by Foster (1974, 1989) and by Cooper from his studies of species from the subantarctic waters of the Atlantic (1982) and Indian (1981) oceans.

The genera included in the Terebratellinae are similar in folding, sulcate to intraplicate; foramen position lies within the range submesothyrid–mesothyrid–permesothyrid; the loop is either free or with transverse bands connecting the descending branches and the septum; the shell may be smooth, partially or fully ribbed. The only consistent associations of characters appear to be foramen type with shell thickness, a submesothyrid foramen with an unthickened shell and a permesothyrid foramen with a thickened shell (thick shells however are not necessarily permesothyrid). The shells of species with a mesothyrid foramen may be differentially thickened (*Neothyris*, all species), unthickened (*Magellania flavescens*, *M. fragilis*, *M. joubini*) or variable in thickening (*Magellania macquariensis*, *M. kerguelensis*, *M. venosa*, *Terebratella dorsata*).

The difficulties in separating terebratelline lineages is well illustrated by those species which have been attributed to *Magellania* by Foster (1974, 1989). Cooper (1981) considers that the species *macquariensis* and *kerguelensis* should be placed in *Aerothyris* and Zezina (1985) has placed *spinosa* in her new monotypic genus *Fosteria*. (Foster, in 1974, had described the species as very similar to *M. fragilis* and *M. joubini* except in the possession of spinose descending branches. Spinosity occurs to a varying extent in the loop development of

many species and, since members of the species are small, separation on this one morphological feature may not be justifiable.) There seems little doubt, as recommended by Cooper (1981) that *M. flavescens* (the type species) and *M. venosa* should be in different genera and it would be desirable if a worker with access to good collections of *Magellania venosa* would take this step. Foster (1989) states that a better understanding of this species is essential in order to evaluate the number of similar species that occur in the same area and which may be variants of *M. venosa*. They include species of *Aneboconcha*, *Syntomaria* and *Dyscritosia*. Until such a study can be undertaken, morphological and distributional patterns suggest that the most natural grouping of these species would be as follows:

1. *Magellania flavescens*.
2. *Aerothyris macquariensis* and *A. kerguelensis*.
3. *Magellania venosa*, *M. joubini*, *M. fragilis*, *Fosteria spinosa*, *Aneboconcha obscura*, *Dyscritosia secreta*, *Syntomaria curiosa*.

Magellania flavescens is distinguished from all other species by beak characters (long with deltidial plates invariably fused with a round mesothyrid foramen) and ornament. Species of *Aerothyris* are smooth with a short beak, a keyhole mesothyrid foramen and short deltidial plates which are commonly but not invariably disjunct. The third group includes smooth forms with a short beak, submesothyrid to mesothyrid foramina and deltidial plates that are short and commonly conjunct in species that are moderate to large in size (*Magellania venosa*, *M. joubini*, *M. fragilis*) and rudimentary in species that are small in size (*Fosteria spinosa*, *Aneboconcha smithi*, *A. obscura*, *Syntomaria curiosa*, *Dyscritosia secreta*). *Pirothyris* was included in the Anakineticinae (Richardson 1991) on the form of the cardinal process although earlier studies on the development of *P. vercoi* (Richardson 1975) had shown that inner hinge plates form and thicken early in ontogeny. *Pirothyris* is an atypical terebratellid with links to the Terebratuloidea in shell shape (depth greater than width) and folding (uniplicate) and cases could be made for including it in either the Anakineticinae or the Terebratellinae.

SUBSTRATE RELATIONSHIPS

Knowledge of the substrate relationships of species is of the greatest importance in any family study firstly because distribution is governed by the capacities of different species to colonise substrates, secondly because of the strength of the correlation between substrate type, morphology

and life style. The strength of this association in articulate brachiopods is evident in the numerous instances of homeomorphy they provide.

All terebratellid species are pediculate but they differ in relationships with the substrate and these differences are evident in the variability of the pedicle and of its housing—the beak and cardinalia. Some species are generalist in character and occupy an apparently unlimited range of substrates, others are highly specialised forms which function only in a particular type of sediment.

Species defined as generalist have the capacity to settle and survive on substrates of any size. In these species the pedicle functions as a pivot when bonded with large substrates and as a moving part when bonded with small (Richardson 1986). Therefore life style varies according to the size of the substrate used for settlement, bondage with a large substrate such as a rock face resulting in a sedentary life style, bondage with a small (relative to shell size) substrate in free life on the sea floor. The movement of either the shell or the pedicle (with its bonded substrate) prevents the build-up of sediment on the shell surface. The phrase 'bonded substrate' is used in preference to 'attached substrate' because of the confusion associated with the latter. The word 'attach' has been used to describe the union between the pedicle and substrate and also as an adjective synonymous with pediculate and sedentary, i.e. an attached brachiopod. Many adult articulates retain the larval substrate but live as free forms on soft sediments and would therefore be described as both permanently attached and free. Thus, 'attach' and all its derivatives perpetuate the falsity of the assumption that articulate brachiopods are uniform in life style and that free brachiopods are 'fallen' forms.

The generalist species most extensively studied *in situ* is *Magasella sanguinea* (Richardson 1981a, 1981b; Foster 1989). It is a common inhabitant of shallow subtidal waters in New Zealand, both on rock faces (sedentary individuals) and the sea floor (free individuals) where it is as common in mud as in coarser sediments. Free individuals are found lying on either valve. The shell is invariably unthickened, biconvex, the beak short with a large submesothyrid to mesothyrid foramen. It is highly variable in shape and size and, in these and other attributes, closely resembles *Terebratalia transversa* (Schumann 1991) and *T. coreanica* (Richardson et al. 1989), examples of generalist species from the Laqueidae and which occupy eastern and western shorelines of the northern Pacific Ocean.

Generalists are found in areas in which sites for settlement show a wide variation in size; i.e. they occupy shoreline areas or shelf sediments in which the components vary in size; e.g. the till of Antarctic shelves. They may also be retrieved, although not in large numbers, from shelf sediments of more uniform grain size. For example, the distribution of *Magellania flavescens* on shelf sediments has been studied in southern Australia where the middle and outer shelf is covered with bryozoan sands. *M. flavescens* has been dredged from this area together with forms specialised for this particular sediment (Richardson 1987). However, collections by scuba in this high energy environment show that *M. flavescens* occurs only as a sedentary form, individuals being bonded to the scattered reefs and outcrops that occur on the shelf. Specimens from these areas are smaller and squatter than individuals from shoreline habitats.

Of the living terebratellid species studied none, like the micromorphic members of the Kraussinidae, Megathyrididae and Platidiidae are exclusively sedentary in habit. All members of the Bouchardiinae and Anakineticinae are free forms specialised for life in bryozoan sands. Members of the Terebratellinae are more varied morphologically and less specialised in life style. Two genera, *Neothyris* and *Gyrothyris*, are free forms which do not appear to be specific to a particular sediment, they are invariably thickened with a mesothyrid foramen and a variably curved beak. The remaining taxa are generalist to the extent that they appear to live as either free or sedentary individuals but shape, size range, pattern of distribution all indicate tendencies towards one or other life style. For example, *Magasella sanguinea* is as common on soft sea floors as it is on hard substrates, whereas species of *Calloria* are more commonly found (Stewart 1981; Doherty 1979) on rocky substrates. Stewart has shown that differences in the habitats of populations of *C. inconspicua* are also evident in the mean size and shape of individuals.

All other terebratelline taxa are known from dredged material only. Species of *Aerothyris*, *Magellania venosa*, *Terebratella dorsata* are all variably thickened which would suggest that they occur predominately, if not exclusively, on soft sediments. They are not as specialised for free life as species of *Neothyris* and *Gyrothyris* in which shell thickening is of early inception and invariably present. Unthickened dredged forms (*Syntomaria*, *Aneboconcha*, *Dyscritosia*) occur in the size range recorded for *Calloria*. They were collected (Cooper 1982) from the vicinity of islands in the South Atlantic and Foster (1989) considers that they may represent young populations of *Magellania venosa*.

Differences in the capacity for colonisation are important to note in any studies of dispersal. Since

generalists have the capacity to colonise substrates of any type they are also less affected by environmental events that cause changes in substrates. Specialists can colonise only those substrates that they are morphologically adapted to occupy. The patterns of settlement and survival in one area illustrate the latter point. New Zealand's Paterson Inlet contains 4 species all of which settle at random on surfaces of any size and composition (Richardson 1981a). Only the generalists (*Magasella sanguinea* and *Calloria inconspicua*) survive as adults on larval substrates of any size, one species (*Notosaria nigricans*) is restricted to large substrates, the other (*Neothyris lenticularis*) to small.

DISTRIBUTION

With the exception of the Trigonoseminae, the subfamilies of the Terebratellidae are confined to the Southern Hemisphere between Antarctic shorelines and latitudes of approximately 30°S and, with the exception of 2 genera, to the Cainozoic era. The subfamilies Bouchardiinae and Anakineticinae contain a larger number of fossil than living genera while the Terebratellinae contains more living than fossil. The earliest fossil genera of the Bouchardiinae (*Bouchardiella*) and the Anakineticinae (*Australiarcula*) occur in the Cretaceous while the Australian Eocene genus *Diedrothyris* is the oldest terebratelline known. Living Bouchardiinae occur only in Brazil, Anakineticinae in Australia while the Terebratellinae occur around the coasts and on the shelves of all land masses found between the Antarctic and latitudes of 35°S.

Foster (1974) showed that members of the Terebratellinae exist in very large numbers in the Southern Hemisphere in areas shallower than 1000 m and noted that *Magellania fragilis* and *M. joubini* are the most prominent species on the entire antarctic shelf. The map of distribution (Fig. 4) of the Terebratellinae is derived from Foster's figure (1974, p. 31) and has been extended to include the Australian species *Magellania flavescens* and Cooper's genera *Dyscritosia*, *Aneboconcha*, *Syntomaria* and *Calloria*.

The bathymetic range at which many species are found may be correlated with shelf depth. For example, the Ross Sea shelf is wide and deep (100 to 1000 m) and species occur at all depths. The New Zealand shelf and neighbouring rises (Chatham Rise, Campbell Plateau) rarely exceed depths of 400 m. *Magellania venosa* is most common at shelf depths approximately 300 m) but has been recorded from 5 to 1900 m and is the only terebratelline species known from the

slope. *Terebratella dorsata* commonly occurs with *Magellania venosa* on the shelf but has not been recorded from the slope.

All terebratelline species appear to live on varied shelf substrates and *in situ* observations in Australian and New Zealand waters show that they may be occupied by free (*Neothyris*, *Gyrothyris*) or free and/or sedentary forms (*Magellania flavescens*, *Magasella sanguinea*, *Calloria inconspicua*). The sites from which *Aerothyris kerguelensis* has been collected are recorded (Cooper 1981) as gravels, coarse and fine sands and muds. The greater part of the Ross Sea shelf is covered with till—unsorted material ranging from rock flour to boulders.

Fossil members of the Bouchardiinae and Anakineticinae occupy the same type of sediment in the same geographical areas as living members. *Bouchardia rosea*, the only living species of the Bouchardiinae, occurs in bryozoan sands off Brazil (Tommasi 1970). Mancenido & Griffin (1988) note that records of the genus range from Palaeogene (palaeolatitudes of 75°S to Neogene of 45°S) and that the present position of the genus at 35°S indicates displacement in a northward direction along the eastern margin of South America. The distribution of one member of the Bouchardiinae, *Neobouchardia minima*, is significant — it has not been recorded from modern seas but conspecific populations occur in the Oligocene–Pliocene of both New Zealand and Australia (Richardson 1973).

Living anakineticinids are found only in the bryozoan sands of the southern Australian shelf and these communities replicate those found in Australian Eocene–Pliocene calcarenites (Richardson 1991). New Zealand Oligocene deposits contain numerous species of each of 2 anakineticinid genera, *Magadina* and *Rhizothyris*, none of which have survived the reduction of shallow marine shelf environments during regressive phases in the Miocene. Like the Australian anakineticinid genera they were forms that were specific to carbonate sands.

New Zealand is the most valuable source of information on the distribution of living and fossil Terebratellinae. In the first place, all those genera with living species also occur in Tertiary deposits, secondly, abundant fossil deposits (shelly limestones) contain aggregates of species that replicate the brachiopod assemblages found in habitats on modern rocky shorelines (Richardson 1984). Similar deposits are rare components of the fossil record in other parts of the world. Two groups of genera can be distinguished in the New Zealand record. The first consists of extinct genera (*Waiparia*, *Stethothyris*, *Pachymagas*) all of which

show the morphological characteristics of forms specialised for a free life and which are known only from the Late Oligocene to Middle Miocene. The second group consists of genera with both living and Tertiary species (*Magasella*, *Calloria*) which are common at or near modern rocky shorelines and in Eocene and Oligocene shelly limestones (Allan 1960; Richardson 1984). Species of *Neo-*
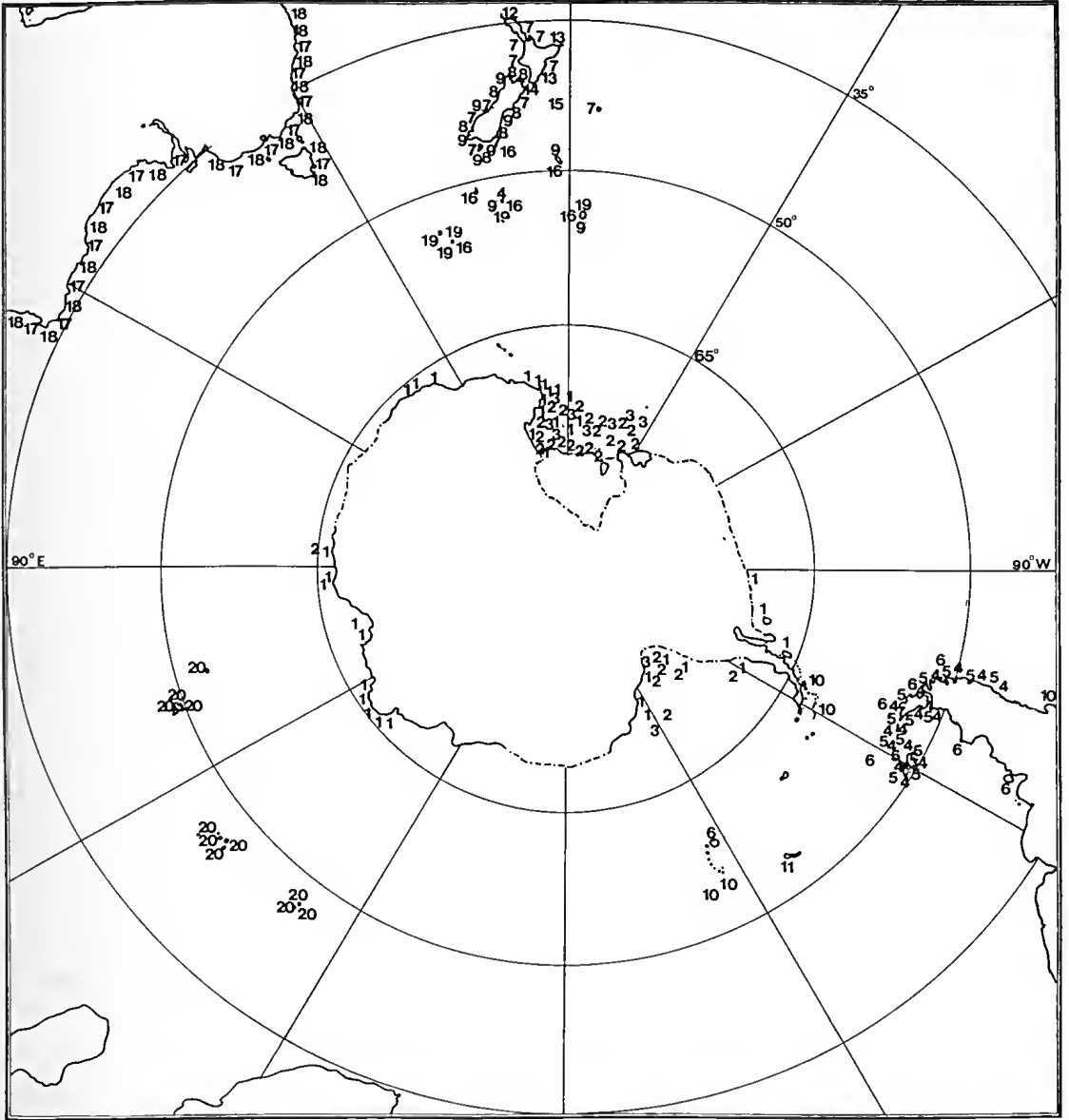
Fig. 4. Distribution of the species of the subfamily Terebratellinae from the records of Cooper (1973, 1981, 1982), Cooper & Doherty (1993), Foster (1974, 1989), McCammon (1973), Richardson (1981a, 1987).
1, *Magellania joubini*; 2, *Magellania fragilis*; 3, *Fosteria spinosa*; 4, *Terebratella dorsata*; 5, *Magellania venosa*; 6, *Aneboconcha obscura*; 7, *Calloria inconspicua*; 8, *Magasella sanguinea*; 9, *Neothyris lenticularis*; 10, *Syntomaria curiosa*; 11, *Dyscritosia secreta*; 12, *Calloria variegata*; 13, *Magasella haurakiensis*; 14, *Neothyris compressa*; 15, *Neothyris dawsoni*; 16, *Gyrothyris mawsoni*; 17, *Magellania flavescens*; 18, *Jaffaia jaffaensis*; 19, *Aerothyris macquariensis*; 20, *Aerothyris kerguelensis*.

thyris are found in a variety of originally soft sediments from the Pliocene and Pleistocene periods (Allan 1960; Neall 1972).

Australian Tertiary deposits consist almost exclusively of originally soft sediments. As noted above, an almost continuous Tertiary record of anakineticinids is available from the Eocene period. In addition, a number of terebratelline genera occur in sediments deposited during the Oligocene and Miocene in embayments of the southern coastline—the Otway, Gippsland and Murray basins. These genera were specialised to varying degrees for soft sediments (limestones). The only living terebratellines found in Australian waters are *Magellania flavescens* and *Jaffaia jaffaensis*.

Foster (1974) records that brachiopods similar or identical to the Recent South American species *Magellania venosa* and *Terebratella dorsata* occur in Antarctic strata of Oligocene and Miocene age. No fossil records are known of *Aerothyris*, *Aneboconcha*, *Dyscritosia*, *Syntomaria*.

All terebratelline genera, living and fossil, are endemic with the single exception of *Stethothyris sufflata*. This species, like another form (*Neobouchardia minima*) specialised for free life in carbonate sands occurs in Oligocene deposits of both Australia and New Zealand.

In general then, members of the southern subfamilies of the Terebratellidae appear to be consistent in nature and distribution and in their response to environmental changes. They occupy rocky shorelines and shelves but not the slopes (with the exception of *Magellania venosa*) or the abyss and similar forms occur in similar habitats. Species with specialist characters occur only in sediments of a specific nature (although generalists may also occur therein), e.g. greensands, bryozoan sands. As could be predicted, response to environmental change differs in generalist and specialist forms. The New Zealand record shows the sediment changes that accompanied Miocene regressions led to the extinction of all specialists for soft sediments while generalists appear to have occupied shoreline habitats since the Eocene. Members of both the Anakineticinae and Bouchardiinae are all substrate-specific forms and so are limited in distribution. The Terebratellinae are not substrate specific and are widely distributed within the Southern Hemisphere.

ORIGINS

The origins and the means of distribution of the Terebratellidae have been discussed by Thomson (1918), Blochmann (1908), von Ihering (1903) and Allan (1963). They agree that the probable source of origin was Gondwana and that shallow seas around land bridges would have provided routes for the dispersal of ancestral forms. They came to this conclusion in view of:

1. the unlikelihood that transoceanic dispersal could occur with a non-planktotrophic larva;

2. the endemic nature of the faunas of South America, New Zealand and Australia;

3. the lack of evidence of land bridges connecting these southern lands during the Tertiary.

This view of the distribution of southern faunas has not substantially altered. Plate tectonics, of course, has provided the means of distribution without the need to postulate land bridges. It has also been shown that substrate type, in addition to the length of larval life, is a limiting factor in distribution (Richardson 1986). While the broad view of terebratellid distribution is shared with earlier workers, recent work on the subfamily Terebratellinae has made it possible to make a more educated guess as to the nature of ancestral stock.

Work on the Terebratellidae in all parts of their geographical range has shown consistency in patterns of distribution with the nature of species. Undifferentiated or generalist species may be widely distributed (with geography and substrate) and they are variable in those characters linked with the environment (differential thickening, beak characters, shape and size). Species specialised for shelf sediments are limited in distribution and are less variable morphologically, both distribution and variability being related to extent of specialisation.

It seems unlikely that the patterns of distribution of terebratellid brachiopods in earlier periods would differ appreciably from those evident throughout the Cainozoic. In other words, given the evidence available, the most valid working hypothesis is that the shorelines and shelf of Gondwana would have been occupied by generalist species and by species specialised to varying degrees for shelf life. With the break-up of the continent their survival would have been related to the extent of substrate loss or change. Differences in the requirements of generalists and specialists means that generalists are more likely to survive periods of environmental change as illustrated by the extinction of all taxa specialised for shelf sediments during a period of instability in the New Zealand Miocene.

The break-up of Gondwana together with the differential survival of species would account for the present distribution in which generalists and near-generalists occur around all Gondwana-derived land forms. The only specialists shared are 3 conspecifics (1 cancellothyrid and 2 terebratellid

speeies) and, since all were adapted for life in carbonate sands, it is likely that some part of the Gondwana shelf contributed to the shelves of Australia and New Zealand. All other specialists found in southern latitudes are endemics; i.e. they evolved in the area they now occupy. The derivation of species of one of the endemic genera, *Neothyris*, has been referred to by Neall (1972) and Aldridge (1991) and a detailed analysis of the direction of evolution in this genus is in preparation.

The difficulty all workers have experienced in separating the non-specialist members of the subfamily Terebratellinae is an indicator of the close relationship existing between species now attributed to *Terebratella, Magellania, Aerothyris, Fosteria, Syntomaria, Aneboconcha, Dyscritosia, Calloria, Magasella*. These similarities are the result of relatedness not of convergenee beeause they occur in sets of characters which appear to be independent of the environment. Morphological differences are most pronounced in Australian and New Zealand speeies which differ from each other and from South American and Antaretic species to a greater extent than any of the latter differ from each other. Australia and New Zealand arc also the most isolated land forms whereas chains of islands form shallow connections between South America and Antarctica. Morphological differences may therefore be associated with greater isolation during the Cainozoic. Differences may also have resulted from the nature of the generalist stock that occupied different parts of the Gondwana coastline. In both Australia and New Zealand populations of *Magellania flavescens, Calloria inconspicua* and *Magasella sanguinea* vary with either or both geography and habitat (Stewart 1975, 1981; Aldridge 1981). For example, 3 geographical variants of *Magasella sanguinea* occur on different coasts — the east coast of the North Island, the west coast of the North Island, all eoasts of the South Island together with the south coast of the North Island. A hypothetical break-up of New Zealand would mean that slightly different stoeks would be separated aecording to the lines of fracture.

DISCUSSION

Chronologically, the Terebratellidae is the youngest articulate family and comparison of its character with that of older families is of interest in view of the repetitive history of articulates (Cooper 1970; Rudwiek 1970). Families of the Rhynchonelloidea and the Terebratuloidea are cosmopolitan and abyssal and members may be widely separated whereas the Terebratellidae are coneentrated in the area of their presumed origin and no taxa have been collected from bathyal or abyssal waters. The restricted distribution of the Terebratellidae throughout their history also makes it unlikely that they would have originated with all other members of the Phylum in seas at low latitudes as suggested by Zezina (1985). An origin in low latitudes would require extensive transoceanic travel which seems unlikely given the brevity of larval life and the substrate specificities of some members.

Family evolution is a field in whieh little conjceture has been possible because of the difficulty in older families of establishing the nature of relationships between species. Relationships in these families are masked by a eombination of age, stasis, convergence and by the paucity of living members. Older families are eosmopolitan and, as a rule, their members do not occur in abundancc. The Thecideoidea, Rhynchonelloidae, Cancellothyroidea, Terebratuloidea were all more common in past eras — numbers of genera in the Rhynehonelloidae, for example, declined from 113 in the Jurassic to 17 in the Reeent, the Terebratuloidea from 136 to 19 in the same periods (Cooper 1988). Age, together with sparse occurrence and cosmopolitan distribution means that the present eomposition of these superfamilies is unrepresentative, i.e. they are remaindered groups which have shown no evidence of diversification since, at least, the Jurassic (Cooper 1988) and therefore relationships between species and genera would be impossible to determine. As a consequence, the present eomposition and distribution of non-terebratelloid families ean provide little information on origins and paths of dispersal of artieulates. The degree of specialisation of the tcrebratellid subfamilies Bouehardiinae and Anakineticinae also makes any analysis of relationships difficult.

More produetive ground for conjecture is provided by the Terebratellinae. Since a substantial amount of information on ecology is now available, faetors other than preservable hard parts can be ineluded in any assessment; e.g. studies of the members of this family have shown that the pcdicle does not function as an anchor chain but as an appendage, that it is highly variable and that its muscles and their function determine the structures of the cardinalia. Therefore, the morphological variability of terebratelline taxa is derived from the variability in substrate relationships that eharacterises generalist taxa. Speeialist taxa with a constant substrate relationship show lower morphologieal variability. Generalist and near-generalist species comprise the bulk of speeies atributed to the Recent Terebratellinae and they appear to have the capaeity to give rise to more

specialised forms by the colonisation of substrates that are less variable than those in shoreline regimes. Evidence that endemic species specialised for shelf sediments may be derived from generalist shoreline stock living in the same area will be examined in detail in a forthcoming paper on the species of *Neothyris* and *Magasella* now living in New Zealand waters.

It is of interest to note the distribution with depth of species from different families. Members from families belonging to the Rhynchonelloidea and Terebratuloidea occur on the shorelines and/or shelves of both Australia and New Zealand and, in addition, have been collected from abyssal sediments of the Tasman Sea whereas members of the Terebratellidae are known only from the continental shelves. This pattern suggests that a correlation may exist between family age and extent of distribution with depth. It gives some support to the present supposition of the shoreline as a generative zone with direction of spread from shoreline to shelf to slope to abyss.

A pattern of distribution similar to the Terebratellidae is evident in laqueid genera from the north Pacific rim. Generalists are found around shorelines and it appears that diversification of this stock has resulted in species specialised for different shelf sediments in Japan and California, e.g. a generalist stock similar to *Terebratalia coreanica* is considered to be ancestral to the shelf species *Coptothyris grayi* (Nomura & Hatai 1936). Members of the Laqueidae are not known from northern or southern circum-polar seas, the Atlantic or from abyssal sediments. It is significant that the Terebratellidae and Laqueidae are the most localised and are also the youngest articulate families.

Integration of the information now available shows that the history and present distribution of the family can best be accounted for by the redistribution of generalist stock with the Gondwana shoreline. The differentiation of this stock for particular substrates has occurred in areas that now differ in degrees of isolation, in the range of sediments available and in tectonic stability. Determination of the character of terebratellid faunas by these variables is well illustrated from the Australian and New Zealand records. Carbonate sands and bioelastic limestones were deposited in both regions during the early to middle Tertiary and they contained large assemblages of terebratellids (anakineticinids and terebratellinids) specialised for free life. The drastic reduction of shallow marine shelf environments with plate movement during the Miocene in New Zealand resulted in their extinction whereas the greater stability of Australia and the retention of carbonate sands has meant that assemblages (almost exclusively anakineticinids) in modern seas replicate those found in Tertiary deposits. The modern terebratellid fauna of New Zealand consists exclusively of members of the subfamily Terebratellinae and species of only 2 genera (*Neothyris, Gyrothyris*) may illustrate early stages in the process of adaptation for the terrigenous sediments that now surround New Zealand.

ACKNOWLEDGEMENTS

REFERENCES

ALDRIDGE, A. E., 1991. Shape variation of *Neothyris* (Brachiopoda, Terebratellinae). In *Brachiopods through Time*, Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 5–9 February 1990, eds D. I. MacKinnon, D. E. Lee, J. D. Campbell: 115–122.

ALLAN, R. S., 1940. A revision of the classification of the terebratelloid Brachiopoda. *Records of the Canterbury Museum* 4: 267–275.

ALLAN, R. S., 1960. The succession of Tertiary brachiopod faunas in New Zealand. *Records of the Canterbury Museum* 7: 233–268.

ALLAN, R. S., 1963. On the evidence of austral Tertiary and Recent brachiopods on Antarctic biogeography. In *Proceedings of the 10th Pacific Science Congress* 1961, Bishop Museum Press, 451–454.

BLOCHMAN, F., 1908. Zur Systematik und Geographischen Verbreitung der Brachiopoden. *Zeitschrift fur wissenschaftliche Zoologie* 90: 596–644.

COOPER, G. A., 1970. Generic characters of brachiopods. In Proceedings of the North American Paleontological Association, Field Museum of Natural History, Chicago, September 5–7, 1969, vol. 1, E. L. Yochelson, ed., Allen Press, Lawrence, Kansas: 194–263.

COOPER, G. A., 1973. Vema's Brachiopoda (Recent). *Smithsonian Contributions to Biology* 17: 51 p.

COOPER, G. A., 1981. Brachiopoda from the southern Indian Ocean (Recent). *Smithsonian Contributions to Biology* 43: 92 p.

COOPER, G. A., 1982. New brachiopods from the Southern Hemisphere and *Cryptopora* from Oregon (Recent). *Smithsonian Contributions to Biology* 41: 43 p.

COOPER, G. A. & DOHERTY, P. J., 1993. *Calloria variegata* n. sp., a new Recent species of brachiopod from northern New Zealand. *Journal of the Royal Society of New Zealand* 23: 271–281.

DOHERTY, P. J., 1979. A demographic study of a subtidal population of the New Zealand articulate brachiopod, *Terebratella inconspicua*. *Marine Biology* 52: 331–342.

ELLIOTT, G. F., 1965. Subfamily Trigonoseminae Elliott, n. subfam. In *Treatise on Invertebrate Paleontology*, Part H, *Brachiopoda*, vol. 2, R. C. Moore, ed., Geological Society of America and University of Kansas Press, Lawrence, Kansas, 851–854.

ENDO, K., 1987. Life habitat and relative growth of some laqueid brachiopods from Japan. *Transactions of the Proceedings of the Palaeontological Society of Japan* 149: 180–194.

FOSTER, M. W., 1969. Brachiopoda in Distribution of selected groups of marine invertebrates in waters south of 35°S latitude. Antarctic Map Folio Series, Pl. 9. American Geographical Society, New York.

FOSTER, M. W., 1974. Recent Antarctic and subantarctic brachiopods. *Antarctic Research Series* 21. American Geophysical Union, Washington D.C.: 189 p.

FOSTER, M. W., 1989. Brachiopods from the extreme South Pacific and adjacent waters. *Journal of Paleontology* 63: 268–301.

IHERING, H. VON, 1903. Les brachiopods Tertiares de Patagonia. *Anales Museo Nacionale Buenos Aires*, ser 3A, vol. 2: 321–349.

McCAMMON, H. M., 1973. The ecology of *Magellania venosa*, an articulate brachiopod. *Journal of Paleontology* 47: 266–278.

MACKINNON, D. I., 1987. The influence of Australian-Antarctic plate tectonics and palaeoceanographic development on the morphology and inferred life habits of New Zealand Neogene brachiopods. *Palaeogeography, Palaeoclimatology, Palaeoecology* 58: 63–73.

MANCENIDO, M. O. & GRIFFIN, M., 1988. Distribution and palaeoenvironmental significance of the genus *Bouchardia* (Brachiopoda, Terebratellidina): its bearing on the Cenozoic evolution of the South Atlantic. *Revista Brasileira de Geosciencias* 18: 201–211.

NEALL, V. E., 1972. Systematics of the endemic New Zealand brachiopod, *Neothyris*. *Journal of the Royal Society of New Zealand* 2: 229–247.

NOMURA, S. & HATAI, K. M., 1936. A note on *Coptothyris grayi* (Davidson). Saito Ho-on Kai Museum Research Bulletin 10: 209–217.

OWEN, E. F., 1977. Evolutionary trends in some Mesozoic Terebratellacea. Bulletin of the British Museum (Natural History) Geology 28: 207–254.

RICHARDSON, J. R., 1973. Studies on Australian Cainozoic brachiopods 3. The subfamily Bouchardiinae (Terebratellidae). *Proceedings of the Royal Society of Victoria* 86: 127–132.

RICHARDSON, J. R., 1975. Growth patterns of the loop and cardinalia in five Recent terebratellid species. *Proceedings of the Royal Society of Victoria* 87: 197–206.

RICHARDSON, J. R., 1980. Studies on Australian Cainozoic brachiopods 5. The genera *Victorithyris* Allan and *Diedrothyris* nov. *Memoirs of the National Museum of Victoria* 41: 43–52.

RICHARDSON, J. R., 1981a. Recent brachiopods from New Zealand—background to the study cruises of 1977–1979. *New Zealand Journal of Zoology* 8: 133–143.

RICHARDSON, J. R., 1981b. Brachiopods in mud: resolution of a dilemma. *Science* 221: 1161–1163.

RICHARDSON, J. R., 1981c. Distribution and orientation of six articulate brachiopod species from New Zealand. *New Zealand Journal of Zoology* 8: 189–196.

RICHARDSON, J. R., 1984. Evolution of brachiopods. *National Geographic Society Research Reports*. Projects for 1976. 751–760.

RICHARDSON, J. R., 1986. Brachiopods. *Scientific American* 254: 100–106.

RICHARDSON, J. R., 1987. Brachiopods from carbonate sands of the Australian shelf. *Proceedings of the Royal Society of Victoria* 99: 37–50.

RICHARDSON, J. R., 1991. Australasian Tertiary Brachiopoda. The subfamily Anakineticinae nov. *Proceedings of the Royal Society of Victoria* 103: 29–46.

RICHARDSON, J. R. & MINEUR, R. J., 1981. Differentiation of species of *Terebratella* (Brachiopoda: Terebratellinae). *New Zealand Journal of Zoology* 8: 163–168.

RICHARDSON, J. R., STEWART, I. R., & LIU XIXING, 1989. Brachiopods from China seas. *Chinese Journal of Oceanology and Limnology* 7: 211–219.

RUDWICK, M. J. S., 1970. Living and fossil brachiopods. Hutchinson University Library, London: 199 p.

SCHUMANN, D., 1991. Hydrodynamic influences in brachiopod shell morphology of *Terebratalia transversa* (Sowerby) from the San Juan Islands, USA. In Brachiopods through Time, proceedings of the 2nd international brachiopod congress, University of Otago, Dunedin, New Zealand, 5–9 February 1990; D. I. MacKinnon, D. E. Lee, J. D. Campbell: 265–272.

STEWART, I. R., 1975. Morphological variation within the Recent brachiopod genus *Magellania*. Thesis submitted for Geology Fellowship Diploma, Royal Melbourne Institute of Technology: 13 p.

STEWART, I. R., 1981. Population structures of articulate brachiopod species from soft and hard substrates. *New Zealand Journal of Zoology* 8: 197–208.

THOMSON, J. A., 1918. Brachiopoda. *Australasian Antarctic Expedition 1911–1914*, scientific reports, series C, vol. 4, part 3: 76 p.

TOMMASI, L. R., 1970. Sobre o braquiopode *Bouchardia rosea* (Mawe, 1823). *Boletin Instituto Oceanografia* 19: 33–42.

ZEZINA, O. N., 1985. Sovremennye brakhiopody i problemy batial'noi zony okeana. Nauka, Moscow: 247 p.

AGE OF AN EARLY DEVONIAN CARBONATE FAN AND ISOLATED LIMESTONE CLASTS AND MEGACLASTS, EAST-CENTRAL VICTORIA

RUTH MAWSON & JOHN A. TALENT

Centre for Ecostratigraphy and Palaeobiology, School of Earth Sciences, Macquarie University, New South Wales, 2109

MAWSON, R. & TALENT, J. A., 1994:12:31. Age of an Early Devonian carbonate fan and isolated limestone clasts and megaclasts, east-central Victoria. *Proceedings of the Royal Society of Victoria* 106: 31–70. ISSN 0035-9211.

Conodont data are presented for stratigraphic sections through Early Devonian carbonate units of the Coopers Creek Limestone in the Tyers–Boola area, and for isolated limestone megaclasts, and limestone boulders from debris-flows in the Early Devonian flyschoid sequences in the nearby Deep Creek–Marble Creek and Platina–Coopers Creek areas of east-central Victoria.

The conodont data from the Tyers–Boola area indicates that, *contra* traditional views, the limestones of this area do not represent a single conodont zone (*sulcatus* Zone) but span parts of two conodont zones as well as all of two others, from late in the *sulcatus* Zone to early in the *dehiscens* Zone, spanning most of the Pragian and extending into earliest Emsian, i.e. 30% or so of Early Devonian time. It is argued that the rich shelly fauna of the uppermost Boola Formation is probably very early Pragian.

Conodonts from richly fossiliferous limestone boulders in debris flows and from isolated megaclasts in the Platina–Coopers Creek and Deep Creek–Marble Creek areas in the southern part of the Walhalla Synclinorium, though mostly not compelling as to age, include a megaclast (Evans Quarry, Coopers Creek), at the base of the Wilson Creek Shale, with a *kindlei* Zone (mid-Pragian) conodont fauna. The age indicated for the Wilson Creek Shale, and thus presumably for entry of the regionally important graptolite *Monograptus thomasi thomasi*, characteristic of it, is no older than *kindlei* Zone. Other limestone boulders and megaclasts of the region appear to be early Pragian or even Lochkovian, antedating the onset of carbonate sedimentation in the vicinity of the Tyers–Boola carbonate fan. They are evidence for a former tract or tracts of shallow water carbonates (a 'lost' carbonate platform) accumulated during the Lochkovian–early Pragian, and lithified prior to incorporation in the Boola, Wurutwun and Wilson's Creek formations. Other evidence suggests this landmass, with exposed Cambrian greenstones, lay to the south of the Tyers–Boola area. The latest Pragian or perhaps earliest Emsian limestone megaclasts farther north at Loyola, emplaced in the Norton Gully Sandstone, are substantially younger than any of those of the Platina–Coopers Creek and Deep Creek–Marble Creek areas in the southern part of the Walhalla Synclinorium; they were coeval with the youngest carbonates of the Tyers–Boola carbonate fan.

EARLY Devonian (Pragian and Emsian) limestones are widespread in south-eastern Australia. In an earlier paper (Mawson et al. 1992) attention was directed to sequences about the Pragian–Emsian boundary, primarily the Buchan Caves Limestone and Wentworth Group in eastern Victoria, and the Cavan Formation at Wee Jasper in southeastern New South Wales. Attention is here directed to a group of generally older limestones in the Tyers–Boola, Platina–Coopers Creek and Deep Creek–Marble Creek areas of east-central Victoria. The limestones of the Tyers–Boola area have been interpreted as a carbonate fan (Rehfisch & Webb 1993). Limestone occurrences elsewhere in the southern part of the Walhalla Synclinorium (see Appendix) are regarded as allochthonous; these include isolated megaclasts (Conaghan et al. 1976). Closer investigation of the conodont faunas

from these occurrences was judged worthy for the following reasons:

1. Preliminary sampling of the Tyers–Boola area demonstrated an abundance of Pragian conodonts; these included several previously unreported species and several morphs of *Eognathodus sulcatus* Philip suggesting much of Pragian time might be represented. Globally, there is a dearth of well documented Pragian (mid-Early Devonian) sequences; the Tyers–Boola successions were thus deemed to have potential for yielding data of more than local significance including, possibly, information on the pattern of conodont biofacies during Pragian time.

2. Tyers quarry was the type locality for four new species of conodonts including the zonally important early Pragian form *E. sulcatus*; these

were obtained from a bulk sample representing 'different lithologies exposed in the quarry' (Philip 1965, p. 95) and thus, potentially, an appreciable time-span. Determination of the ranges of these earlier identified forms relative to the newly identified species was therefore desirable. Additionally, re-sampling could provide useful information on intraspecific variation within *E. sulcatus*.

3. Horizons referred to the Coopers Creek Limestone (or Formation) in the past, and to horizons above and below it, include isolated limestone megaclasts as well as debris flows and carbonate fan deposits (Conaghan et al. 1976; VandenBerg 1988; Mawson et al. 1992; Rehfisch & Webb 1993), the last specifically in the Tyers–Boola area. No age-constraining conodont data have been presented for these carbonates apart from a bulk sample from Tyers (Philip 1965), and from megaclasts at Loyola (Cooper 1973a; Mawson et al. 1992).

4. Graptolites, including the widely distributed *Monograptus thomasi* Jaeger, have long been known from the Wilson Creek Shale. The latter was once thought (Baragwanath 1925) to antedate the Coopers Creek Limestone but is now regarded as a facies equivalent of some or all of the Coopers Creek Limestone; neither unit is now included in the Walhalla Group (Vanden-Berg 1988, p. 112–115). Age-data based on conodonts from the Coopers Creek Limestone could thus have implications for correlation of the globally important graptolite faunas.

The following abbreviations are used for conodont genera throughout the text, on figures and tables: *Anc.* = *Ancyrodelloides*, *Amy.* = *Amydrotaxis*, *B.* = *Belodella*, *D.* = *Drepanodus*, *E.* = *Eognathodus*, *I.* = *Icriodus*, *N.* = *Neopanderodus*, *O.* = *Oulodus*, *Pa.* = *Panderodus*, *Pand.* = *Pandorinellina*, *Ped.* = *Pedavis*, *P.* = *Polygnathus*. Abbreviations used for stratigraphic sections are TQ = old Tyers Quarry, and BOO = Boola Quarry. Spot localities sampled are shown on Figs 1–3. It should be noted that wherever the word zone is used in the following text we imply the current zonal scheme for the Early Devonian, based exclusively on conodonts.

SEQUENCES INVESTIGATED:
STRATIGRAPHIC BACKGROUND

Limestone bodies of Early Devonian age occur on several horizons on both flanks of the Walhalla Synclinorium. They and associated coarse clastics were once thought to represent a single horizon (Herman 1901; Whitelaw 1916; Junner 1920;

Baragwanath 1925; Skeats 1928; Thomas 1942) that could be traced from the Loyola occurrences near Mansfield (Cooper 1973a; Mawson et al. 1992) to Tyers, where they disappear beneath the Gippsland Basin. It should be noted that, though these limestones were assumed to be autochthonous, two workers (Murray 1878, 1887, 1895; Kitson 1925) had clearly recognized the discordant relationship between the main limestone bodies and enclosing strata at Marble Creek and Deep Creek. This was prior to recognition that such bodies could, sedimentologically, be far-travelled. Junner (1915) and Thomas (1942) pointed out that the limestone bodies about Coopers Creek occurred on different horizons. Boundaries of the tract interpreted by Thomas as basal conglomerates [= Coopers Creek Formation of Philip 1960a, 1962] of the Walhalla Group, incidentally, differ significantly from the interpretation proffered by VandenBerg (1975 and in VandenBerg & Garratt 1976, Fig. 4.5) where the two main limestone occurrences in the vicinity of Coopers Creek, the White Rock and Evans Brothers' quarries are shown to be about *c.* 100 m apart stratigraphically, the former below and the latter interpreted as occurring within the Wilson Creek Shale. It should be noted that excision of the 'basal conglomerates' from the Walhalla Group (VandenBerg 1977a, 1988) might be viewed as marking a substantial departure from earlier practice in which this unit, regarded as marking a regionally identifiable change in sedimentation, was taken to mark the base of the Walhalla Group (Whitelaw 1916; Skeats 1928; Baragwanath 1925; Thomas 1942; Philip 1960b, 1962, 1968). VandenBerg (pers. comm.) has concluded, from extensive field work, that the 'basal conglomerates' of the above cited authors cannot be aligned precisely from area to area; it is therefore not possible to identify a regional change in sedimentation with any sort of precision.

A major exercise in re-definition of stratigraphic units for the region was undertaken by VandenBerg (1975) as background for revised mapping that covers a broader area, especially to the north, than that considered here. These publications, coupled with a recent synthesis of the stratigraphy and structure of the region (VandenBerg 1988), provide a useful starting point for understanding the stratigraphy of the areas probed in this report. It should be noted that because of difficulties in applying stratigraphic nomenclature from the western to the eastern flank of the Walhalla Synclinorium, a new name, Wurutwun Formation has been introduced for a conglomerate-siltsone interval beneath the Walhalla Group (Carey & Bolger in VandenBerg 1988; Bolger & Carey, in prep.). It should also be

noted that the generally accepted view regarding the turbiditic Walhalla Group and underlying formations of east-central Victoria is that they are primarily deep water (VandenBerg in VandenBerg & Garratt 1976; VandenBerg 1988). A dissenting explanation, that they are shallow marine deposits, nevertheless continues to have its protagonists (Garratt 1983a, p. 123; Weir et al. 1988). Papers on chitinozoans from stratigraphic sections through the limestones in the Tyers and Boola quarries (Winchester-Seeto 1993), and on carbonate petrology of the Tyers–Boola carbonate fan (Rehfisch & Webb 1993) have appeared recently. Manuscripts are in preparation on stratigraphy in the Deep Creek area (Bolger & Carey, in prep.), on dacryoconarids (G. K. B. Alberti, pers. comm.), and on conodonts from autochthonous limestones from the Wilson Creek Shale in Jacob's Creek at Moondarra, and from the Thomson River below Coopers Creek (Carey & Bolger ms.). We are not especially concerned here with questions of priority in application of stratigraphic nomenclature, nor with the possibility of diachronism regionally, though we would submit that there still seem to be substantial difficulties in applying a consistent, high-resolution stratigraphy throughout this south-eastern portion of the Melbourne 'Trough'. Our prime concern is documentation of the conodonts from the Tyers–Boola area, and from various limestone bodies in the southern part of the Walhalla Synclinorium, and probing their chronological and palaeogeographic implications.

1. Tyers–Boola area

Murray (1876, p. 140, 1887, 1889, 1895) was the first to report on the Early Devonian limestones of the Tyers–Boola area (Fig. 1). The occurrence he described is clearly the body cropping out rather poorly in the steep gully informally called Murray's Gully on Fig. 1, a repetition by folding of the main belt of limestones extending through the Tyers and Boola quarries. The latter tract was elegantly surveyed in 1926 by Kenny (1937). The stratigraphy and palaeontology of the entire area were comprehensively investigated by Philip (1960a, 1960b, 1962, 1965). Philip (1960b, 1962) suggested that the boundary between the Boola Beds and the Coopers Creek Limestone should be taken as closely approximating the Silurian–Devonian (Pridoli–Lochkovian) boundary. Subsequently, on the basis of conodonts he concluded that an 'Upper Gedinnian or early Siegenian' age [approximately late Lochkovian–early Pragian in modern parlance] was more likely for the Coopers Creek Limestone (Philip 1965). One must assume, incidentally, that

Philip intended the type sections of his Coopers Creek Formation to be in the vicinity of Coopers Creek, and the type section of his Boola Beds to be in the Tyers–Boola area, presumably one or other of the Tyers River or White's Creek sections, but type sections were not specifically designated. Philip (1960b, 1962) initially believed there had been continuous sedimentation from the Boola Beds into the Coopers Creek Limestone but subsequently (Philip 1965, 1968), on the basis of channels with conglomeratic sediments (including limestone boulders) cut into the Boola Siltstone, suggested unconformable relationships and a major 'regional unconformity' causing 'strata of different ages [to be] brought beneath the Coopers Creek Formation along its strike length' (Philip 1968, p. 915). Subsequent work by VandenBerg (1975, 1988) and others has demonstrated a very different pattern of regional stratigraphic alignments compared with the interpretations presented by Philip, though VandenBerg (pers. comm.) believes channeling of the Boola Formation at the base of the Coopers Creek Limestone may be connected with a minor diastem.

In the Tyers–Boola area, where carbonates predominate over other lithologies in the Coopers Creek Formation (*sensu* Philip), the careful mapping and borehole information presented by Kenny (1937) is indicative of a very important non-carbonate component (conglomerates, shales) and considerable complexity in lithofacies relationships. VandenBerg (1975, 1988), clearly influenced by the predominance of limestone over other lithologies in the Coopers Creek Formation (*sensu* Philip) in the Tyers–Boola area, suggested modification of the name to Coopers Creek Limestone. He had, however, applied the name Coopers Creek Formation to large tracts of siltstone and sandstone, devoid of carbonates apart from rare allochthonous blocks, in the Platina–Coopers Creek and nearby Telbit Crossing areas (VandenBerg & Garratt 1976, Figs 4.4 and 4.5) underlying the Wilson Creek Shale. This clastic sequence was to become the Boola Formation (VandenBerg 1975, 1988, Fig. 4.4), with a designated type section on the Erica–Walhalla road rather than in the Tyers–Boola area. This action effectively made the Boola Formation *sensu* VandenBerg more or less a synonym of the Coopers Creek Formation *sensu* Philip of the Platina–Coopers Creek but not Tyers–Boola area. In addition to being not in accord with Philip's intentions, this action was not in harmony with the spirit of the Australian Code of Stratigraphic Nomenclature. That notwithstanding, we appreciate VandenBerg's pursuit of a regionally consistent stratigraphic framework and have there-
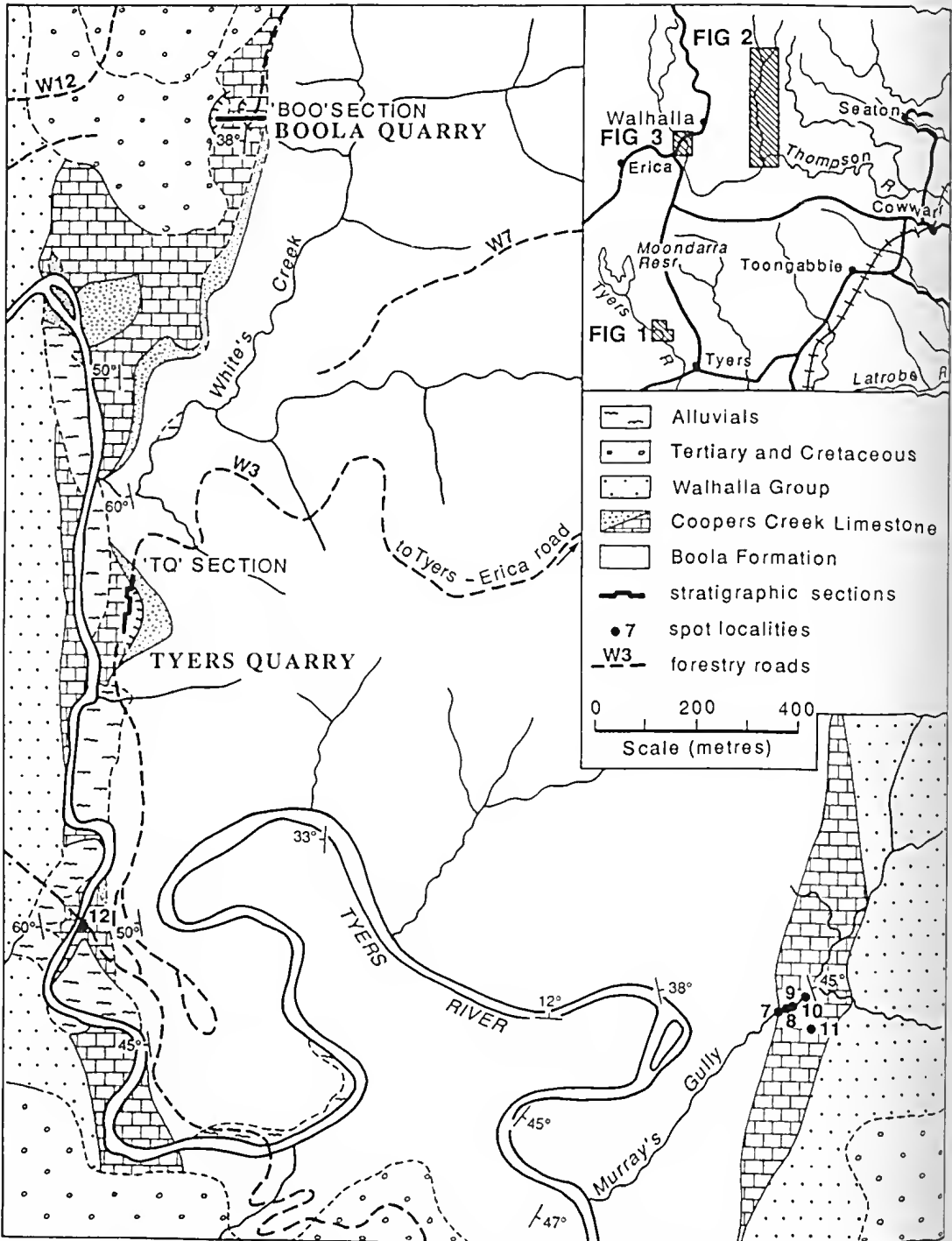
Fig. 1. Geology of the Tyers–Boola area, Victoria, based on mapping by Kenny (1937) and Philip (1962) showing location of stratigraphic sections and spot localities sampled. Note simplified representation of Coopers Creek Limestone: limestones by brick-pattern, mudstones, sandstones and conglomerates by stippling.

fore adopted his recommendations, though with some reservations arising from Kenny's (1937) demonstration of an important non-carbonate component within the carbonate sequence of the Tyers–Boola area. We nevertheless use Vanden-Berg's modification of Coopers Creek Formation to Coopers Creek Limestone, with application restricted to the Tyers–Boola area.

On the basis of thin sections, Chapman (1907) presented preliminary identifications of several species and descriptions of 3 new species from Tyers River (presumably from the old Tyers Quarry): a cyanophyte *Girvanella conferta*, a tabulate coral *Cannapora australis* [=*Favosites squamuliferus* forma *stelliformis* Chapman] and a supposed bryozoan, *Rhombopora gippslandica*; the last is a tabulate coral now referred (Philip 1962) to *Cladopora*. The macrofauna of the Tyers–Boola area was comprehensively described by Philip (1960a, 1962). The taxonomy of some of the rugose and tabulate corals has since been revised (Pedder 1965, 1967; Strusz 1966, 1968; Jell & Hill 1969; Hill 1978), as have the brachiopods (Talent et al. 1993), and the stromatoporoids (Webby et al. 1993). The conodont fauna from Tyers Quarry described by Philip (1965) included a new form, *Eognathodus sulcatus*, which subsequently became the nominate species for the early Pragian *sulcatus* Zone, though inference of the significance of an interval characterized by *E. sulcatus* was made on biostratigraphic data from North America. Cooper (1973b) reported the occurrence of the usually Pragian dacryoconarid *Nowakia acuaria* from limestone in the old Tyers Quarry. The limestones and interbedded clastics of the Tyers–Boola area have been interpreted recently (Rehfisch & Webb 1993) as a primarily carbonate fan, deposited in deep water.

2. Deep Creek, Walhalla

The deeply incised valley of Deep Creek, east of Walhalla, has one salient body of limestone (near the 'Middle Crossing', Fig. 2, loc. 4), closely

Fig. 2. Location of spot samples from Early Devonian carbonates in the watersheds of Deep Creek and Marble Creek, east-central Victoria. The base map is from Vicmap 1:25 000 topographic sheets Beardmore (8122-2-1), Deep Creek (8222-3-3), Porters Creek (8222-3-4) and Walhalla (8122-2-2). Formational boundaries are not shown because recent mapping has resulted in substantial changes in boundaries and nomenclature; this should soon be available (Bolger & Carey ms.). An earlier interpretation of formational boundaries may be obtained from the Geological Survey of Victoria 1:250 000 geological map SJ55-6 Warburton (VandenBerg 1977b).
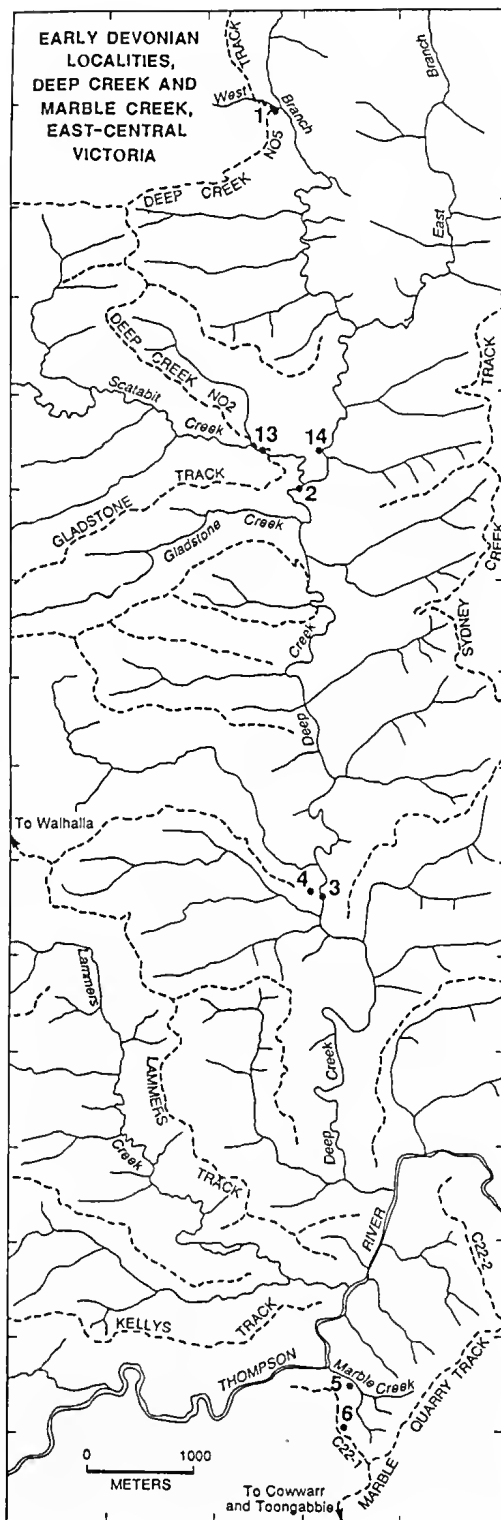
associated with coarse clastics including clasts of fossiliferous limestone. This occurrence, together with the Marble Creek limestones (Fig. 2, locs 5 and 6) and other minor carbonate occurrences on the same general north-south trend would formerly (e.g. Baragwanath 1925, Skeats 1928) have been construed as the eastern belt of fossiliferous conglomerates and grits marking the base of the Walhalla Beds (later Walhalla Group). We have sampled carbonate outcrops at 8 localities in the Deep Creek–Marble Creek tract (Fig. 2); these plot up as occurring in three stratigraphic units on the most recent geological map covering the area (VandenBerg 1977b). Because geological boundaries and stratigraphic nomenclature for the Deep Creek–Marble Creek area will be substantially modified in due course (Bolger & Carey ms.), we have refrained from using former boundaries and nomenclature on Fig. 2. Descriptions of the carbonate occurrences sampled by us, other than the 'Middle Crossing' occurrences (locs 3 and 4) given below, are provided in the Appendix.

An approximately 30×40 m limestone body, interpreted by us as a megaclast, outcrops boldly on the right (west) flank of Deep Creek about 0.25 km upstream from the former 'Middle Crossing', Deep Creek (Fig. 2, loc. 4). This is the limestone which Murray (1878, p. 48, Fig. 4) recognized as discordant and therefore probably Devonian because of 'rest[ing] *on* the upturned edges of the latter ['Silurian strata']. The limestone yields tabulate and rugose corals, is occasionally crinoidal, but seems to be without silicification of fossils. Despite being located *c*. 5.5 km east of Walhalla, this was clearly the limestone in Deep Creek reported by Murray (1878, 1887, p. 45, 1895, p. 38) and source of *Fenestella australis* Chapman and brachiopods referred to *Plectambonites* reported by him (Chapman 1903) from limestones in Deep Creek '7 miles south-east of Walhalla'. Chapman (1912) gave preliminary identifications of material collected by Baragwanath from this limestone body; subsequently he (Chapman 1914) reported a stromatoporoid and 6 species of tabulate corals. It is the type locality for two of these, *Favosites nitida* Chapman [now *Squameofavosites nitidus*] and *Pachypora* [now *Thamnopora*] *alterivalis* (Chapman). Later he (Chapman 1921) described another new species, *Favosites* [now *Emmonsia*] *spinigera* and identified *F. forbesi* Edwards & Haime [= *S. nitidus*] from loc. 4. Two new species of gastropods, *Platyceras minutum*, and *Diaphorostoma* [now *Platyceras (Platyostoma)*] *incisum* described by Chapman (1916) are assumed to have come from loc. 4. These species were revised by Tassell (1977) who, in addition, recorded *Cowwarrella*

cylindrica and *Oriostoma* n. sp. from loc. 4.

Stratigraphically beneath the aforementioned limestone body, outcropping in the bed of Deep Creek, are sandstones and polymict conglomerates, including crinoidal limestone clasts up to 0.5 m across (Fig. 2, loc. 3).

3. Marble Creek
(Old Toongabbie marble quarries)

Kitson (1925) reported on the two richly fossiliferous crinoidal limestone bodies at Marble Creek, formerly quarried for decorative stone. The upper quarry, 'on the brow of a steep hill', was being worked prior to 1887 (Murray 1887, p. 46). Murray had noted that 'downward the limestone disappears, and nothing [i.e. no limestone] can be seen along the face of exposed rock below the quarry' (Murray 1987, p. 46, 1895, p. 38). Kitson noted that the limestone body in the lower quarry, 12.8 m in thickness, is 'not evenly bedded with the slates, but has a very irregular margin, both on the upper and lower side and at the north end' where his figure (Fig. 132) shows the limestone to be abruptly replaced, along strike, by slates. Kitson's and Murray's observations are consistent with interpretation as allochthonous blocks lithified before incorporation in the enclosing argillites (Conaghan et al. 1976, p. 529). Murray (1887, 1895) noted a third body outcropping in Marble Creek, 'a couple of feet long and one foot thick, thinning out to nothing upwards and downwards and entirely enclosed by slates'; an additional minor body of limestone, farther north, was noted by Kitson (1925). Brachiopods (Talent 1956b; Talent et al. 1993), mollusks (Talent & Philip 1956; Tassell 1977, 1982), crinoids (Philip 1961) and a trilobite (Holloway 1991) have been described from the two quarries. Among the new taxa of gastropods proposed by Talent & Philip (1956) were two new genera based on species from Marble Creek: *Cowwarrella* and *Ostlerina*. Knight et al. (1960) placed these in synonymy with *Visitator* Perner and *Platyostoma* Conrad respectively. There is so little similarity between *Visitator* and *Cowwarrella* that we prefer to regard them as discrete and not closely related genera; we believe *Ostlerina* to have value as a distinctly phaneromphalous subgenus of *Platyceras*. No conodonts have been described from the Marble Creek quarries but a sample with a mixture of conodonts from Deep Creek (our loc. 4) and Marble Creek (locs 5 and/or 6) was reported as having *Ozarkodina remscheidensis*, *O. excavata wurmi* and an Se element of ?*Amydrotaxis*, suggesting a late Lochkovian age (Pickett in Holloway 1991).

4. Coopers Creek and Tyers Junction

Limestones have long been known from the Platina–Coopers Creek area (e.g. Murray 1878, p. 48, 1887; Herman 1901; Junner 1915). Thomas (1942) pinpointed 6 significant occurrences of limestones in the area (Fig. 3), two of them sizeable. Both contain abandoned quarries in highly fossiliferous limestones, the White Rock (= Commonwealth Sugar Refineries Quarry) and Evans Brothers' quarries. Unlike the Marble Creek and Middle Crossing Deep Creek limestone bodies, the White Rock occurrence was not a homogeneous body of limestone. VandenBerg (1975) reported it as consisting of 'two tilted limestone megaclasts enclosed in structureless siltstone'. Other limestone megaclasts may have been present. D. E. Thomas (pers. comm., c. 1956) reported the occurrence as having been an agglomeration of discrete limestone blocks that he described as 'giving out' abruptly into mudstone and then back into limestone again, an observation consistent with interpretation as part of a megabreccia or megaconglomerate. The difficulty this presented in mining was said to have been the main reason for its closure c. 1949 (D. E. Thomas, pers. comm.).

McCoy (in Murray 1887, p. 45) gave preliminary identifications of corals, a bryozoan and an ostracode from 'Cooper's Creek' but it was not until 1914 that any taxa were illustrated or described. Chapman (1914) described two new taxa, *Cyathophyllum* [now *Martinophyllum*] *approximans* and *Heliolites interstincta* var. *gippslandica* [now *Pseudoplasmopora gippslandica*] and reported *Favosites forbesi* Edwards & Haime [= *F. coactilis* Philip and *F.* sp.], from limestones from 'Cooper's Creek, behind Chinamen's Garden'; he also reported *F. nitida* Chapman [now *Squameofavosites nitidus*] from 'behind Cooper's Creek copper mine'. The former locality is assumed to have been the limestone lens where Evans Brothers' Quarry is situated, the latter possibly a conglomerate with limestone clasts. Subsequently, Chapman (1921) illustrated *Alveolites regularis* Chapman [= *Favosites squamuliferus stelliformis* Chapman] and identified *Pleurodictyum megastoma* McCoy from unspecified localities at Coopers Creek. Cooper (1971), obtained the zonally important *Eognathodus sulcatus* from a 13 kg sample of limestone from Evans Brothers' Quarry.

SAMPLING

Approximately 1.3 tonnes of samples (5–10 kg each) were obtained from measured stratigraphic sections at the Boola and Tyers quarries, and from
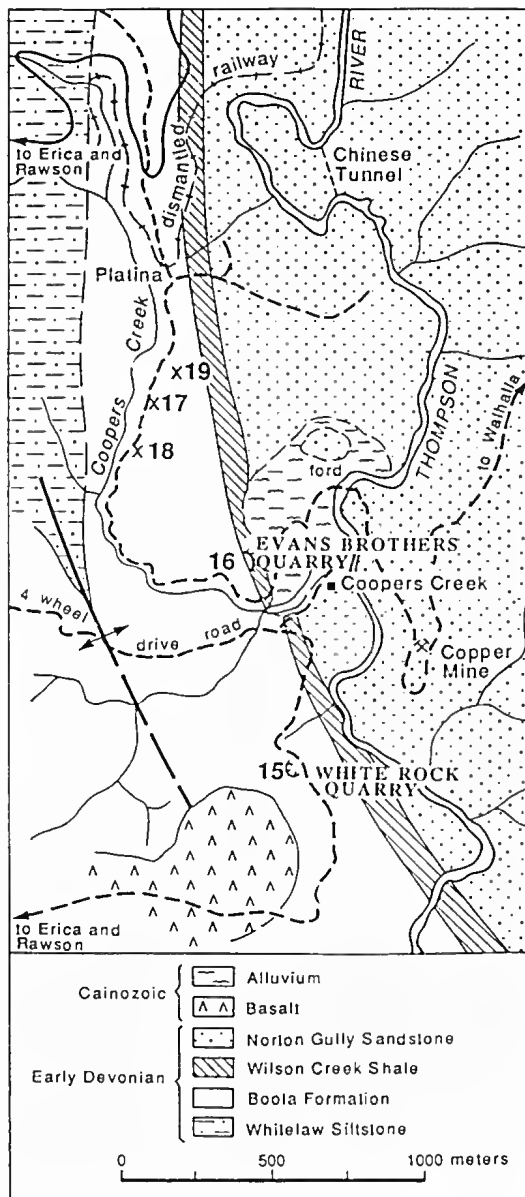
Fig. 3. Location of spot samples from Early Devonian carbonates in the Platina–Coopers Creek area, east-central Victoria. Localities are those of Thomas (1942); basemap is from Vicmap 1:25 000 topographic sheet 8122-2-2 Walhalla; formational boundaries and names are those of VandenBerg & Garratt (1976) except that, to bring nomenclature into line with subsequent usage, Coopers Creek Formation *sensu* VandenBerg & Garratt (1976) is replaced by Boola Formation *sensu* VandenBerg (1988).

spot samples from other localities at Tyers, Deep Creek and Marble Creek, and in the Platina–Coopers Creek area (Figs 1–4). Samples that produced no conodonts after leaching 1.5–2 kg were then discarded; most samples proved productive at this stage and were then dissolved completely. Locations of the stratigraphic sections sampled in the Tyers–Boola area are shown in Fig. 1; positions of horizons sampled are indicated on the stratigraphic columns in Fig. 4. Between 60 and 70 kg were collected from the 'Middle Crossing' megaclast on Deep Creek and from limestone blocks in the underlying conglomerate; samples of calcareous flysch from Deep Creek below Scatabit Creek, and from the west branch of Deep Creek proved barren. Large samples were taken from both of the old 'Toongabbie marble quarries' in the Marble Creek area, about 80 kg from the lower quarry and about 40 kg from the lowest part of the upper quarry. Four of Thomas's (1942) six limestones in the Platina–Coopers Creek area were sampled; these and an isolated area of limestone spall were sampled; all produced conodonts sparingly (Table 2). Cobbles of limestone occur in conglomerates at many localities in the meridional belt extending through Coopers Creek, for example 'near the steel bridge over the Thomson River, about two miles north of its junction with Stringer's Creek' (Junner 1915, p. 289) but our attention in this belt was focussed on the main occurrences.

INTERPRETATION OF CONODONT DATA

Productivities of conodonts from the stratigraphic sections and spot samples from the Tyers–Boola area were generally much higher than for most Early Devonian horizons in south-eastern Australia (e.g. Mawson et al. 1992). This is presumably a reflection of the generally deeper water environments represented in what has been preserved of the carbonate fan in that area. Much lower productivities from most limestone bodies farther north, particularly those of the Platina–Coopers Creek area, are assumed to be connected with the generally very shallow environments represented by these clasts and megaclasts.

In the discussion which follows we have, as previously (Mawson et al. 1992), adopted Lane & Ormiston's (1979) refined the conodont zonal scheme for the Pragian. They demonstrated the utility of three intervals: a redefined zone of *Eognathodus sulcatus*, an intermediate zone of
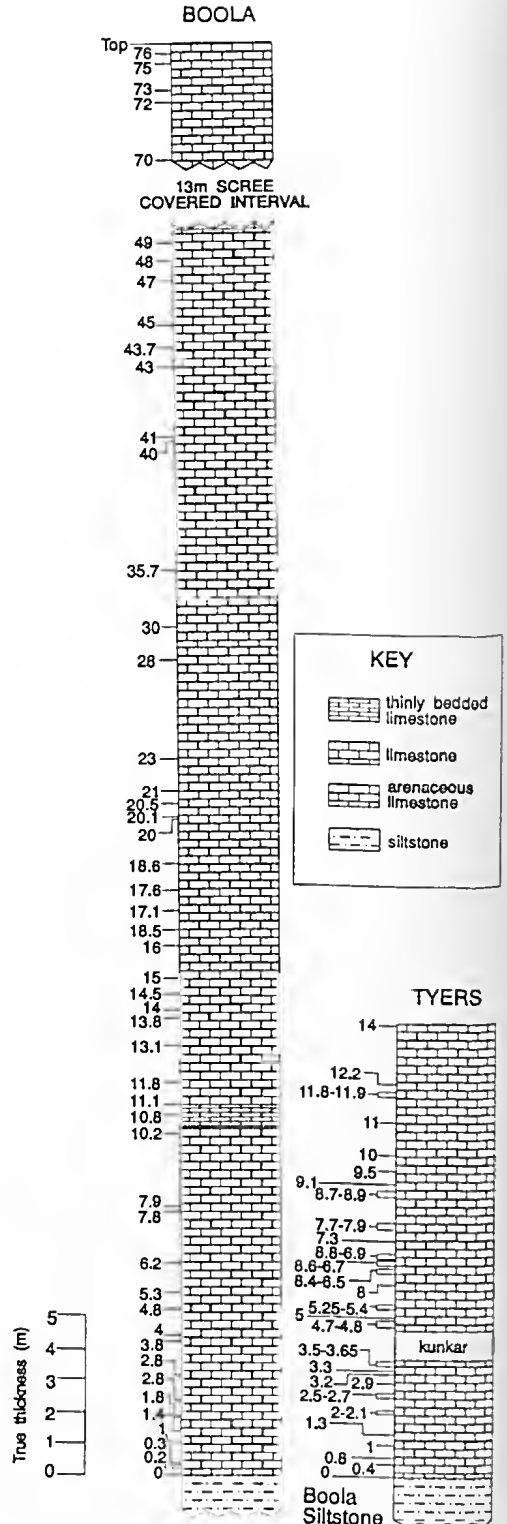
Fig. 4. Stratigraphic sections at Tyers Quarry and Boola Quarry showing horizons sampled.

E. sulcatus kindlei and, as youngest interval, an interval with *Polygnathus pireneae*. The lower boundary of the *pireneae* Zone was defined at the incoming of *P. pireneae*. Due to rarity of both *P. pireneae* and *P. trilinearis*, there may often be difficulties of recognizing the *pireneae* (and/or *P. trilinearis*) interval in the late Pragian. There is still need of an elegant sequence, rich in conodonts, where the transition *Eognathodus* to *Polygnathus* can be documented in detail.

1. Age of the Tyers–Boola carbonate fan

The stratigraphically lowest horizons producing conodonts in the Boola and old Tyers quarries (Fig. 4; Tables 1 and 2) are already *sulcatus* Zone, and not the earliest discernible interval in that zone characterized by *Eognathodus sulcatus eosulcatus* Murphy. That forms typical of the *kindlei* Zone enter low in both stratigraphic sections (7.3 m at Tyers Quarry, 7.8 m at Boola Quarry), and that simplest morphs of *E. sulcatus* are absent from both sections, suggests that much of the *sulcatus* Zone is not represented in the Tyers–Boola area.

Neither *Polygnathus pireneae* nor *P. trilinearis*, the entry of which we would take to be indicators of the *pireneae* Zone, appear in either of our stratigraphic sections. It is therefore possible that the highest parts of both sequences sampled are still within the *kindlei* Zone. Nevertheless, the occurrence of an 'early form' of *Polygnathus dehiscens* from our locality 12 at Tyers demonstrates that the uppermost part of the Coopers Creek Limestone is *dehiscens* Zone (earliest Emsian). We have therefore not exhaustively sampled the uppermost exposures of the Coopers Creek Limestone; limestones from this part of the sequence tend to be massive and yield few if any conodonts. The *pireneae* Zone could well be present but, because of the paucity of conodonts, may not be represented by its indicator species.

Rehfisch & Webb (1993) have interpreted the Coopers Creek Limestone of the Tyers–Boola area as a predominantly carbonate fan deposited, with re-working, into deep water. At least part of the overall sequence, specifically in the vicinity of Boola Quarry, can be interpreted as shallowing upwards. In the upper part of the 'BOO' section at Boola Quarry there is a change to more massive and poorly bedded limestones concurrent with a decline in conodont yield per kg; samples from massive limestones from the hilltop immediately west of the quarry proved barren. We suggest this pattern to be evidence for shallowing upwards perhaps even into a storm-dominated environment.

There is a persistent belief that the Victorian occurrences of *Monograptus thomasi* more or less equate with the *sulcatus* Zone (e.g., Garratt 1983b, p. 85; VandenBerg 1988; Jaeger 1989). For instance, VandenBerg (1988, p. 120) has concluded that '*Monograptus thomasi thomasi* Jaeger is laterally equivalent to the *Eognathodus sulcatus* Zone in the Lilydale Limestone and Coopers Creek Limestone'. In addition, he concluded that horizons represented by *M. aequabilis notoaequabilis*, occurring 'at the top of the Wilson Creek Shale and in the overlying Norton Gully Sandstone' are temporally equivalent to 'the Late Pragian *Polygnathus dehiscens*'. These conclusions were based on much field experience of relatively intractable sequences, on Philip's (1965) work on conodonts at Tyers Quarry, and on an unpublished manuscript (Carey & Bolger ms.) reporting conodonts from two calcareous horizons in the Wilson Creek Shale with an earliest Emsian (not late Pragian) combination of *Polygnathus dehiscens* and *P. pireneae*. Because much, perhaps most of the *sulcatus* Zone is not represented in the Tyers–Boola sequence, and because the sequence extends through the remainder of the Pragian into the early Emsian, from somewhere in (and perhaps high in) the *sulcatus* Zone to at least early in the *dehiscens* Zone, the one-to-one relationship between the *thomasi* and *sulcatus* intervals, as assumed by VandenBerg, cannot be maintained.

Of some interest in this regard is the report by Lenz (1989) of *M. thomasi* in association with *M. yukonensis* and *M. telleri* and his inference that *M. thomasi* is indicative of 'part of the overall *yukonensis* Zone fauna', for which Jaeger (1989) inferred a probable *kindlei* or younger age. It is therefore possible that *M. thomasi* need not have originated until a stage or more later than was once assumed by Victorian workers, i.e. approximately mid-Lochkovian (VandenBerg & Schleiger 1972, Fig. 2). The above data highlight the need for yet another quest for improved time-control through the largely detrital units of central Victoria, an exercise we recognize will not be an easy task.

2. Age of the Boola Formation

The significant shelly faunas of the Boola Formation in the Tyers–Boola area (Philip's 1962, loc. 48 and above) are restricted to the uppermost 45 m of the formation, just beneath the Coopers Creek Limestone. The age assigned to this fauna has fluctuated. Philip (1960b, 1962) at first considered the Boola Formation to be Late Ludlow in age and suggested that the boundary between it and Coopers Creek Limestone should be taken as approximating the Silurian–Devonian boundary.

Table 1. Distribution of conodont elements in section BOO through the Coopers Creek Limestone at Boola limestone quarry.

Table 2. Distribution of conodont elements in section TQ through the Coopers Creek Limestone at the old Tyers limestone quarry and from spot localities from the Tyers–Boola, Deep Creek, Marble Creek, and Platina–Coopers Creek areas.

Discovery of a terebratulid brachiopod, though generically unidentifiable, provided evidence for a Devonian age for the faunas of the uppermost Boola Formation (Philip 1962, Appendix). Subsequently, on the basis of conodonts he concluded that an 'Upper Gedinnian or early Siegenian' age [approximately late Lochkovian–early Pragian in modern parlance] was more likely for the Coopers Creek Limestone (Philip 1965). He (Philip 1965, 1968) also argued for an appreciable diastem between the Boola Formation and the Coopers Creek Limestone. This was accepted by Savage (1973) who referred the faunas of the uppermost Boola Formation to the late but not latest Lochkovian, and placed the Coopers Creek Limestone at about the middle of the Pragian. Garratt & Wright (1989) referred the faunas from the uppermost Boola Formation to their *australis* brachiopod assemblage zone to which they assigned a late Lochkovian age, approximately equivalent to an interval represented by the *pesavis* Zone and the later half of the *delta* Zone. The top of the Boola Formation for them would coincide approximately with the Lochkovian–Pragian boundary; this is a little lower than the position we advocate.

Though, locally, erosional features are apparent at the base of the Coopers Creek Limestone (Philip 1965, 1968; VandenBerg 1988; Rehfisch & Webb 1993), there are other areas, e.g. at the base of our section in Boola Quarry, where sedimentation appears to have been continuous. We are therefore of the opinion that even in areas where erosional channels may be seen at the base of the Coopers Creek Limestone that such channels need not imply a significant diastem (*contra* Philip 1965, 1968). Because the basal beds of the Coopers Creek Limestone are already within the *sulcatus* Zone, we are of the opinion that the locally highly fossiliferous uppermost beds of the Boola Formation in the Tyers–Boola area equate with some or all of the earliest part of the *sulcatus* Zone, including the brief interval characterized by *E. sulcatus eosulcatus*.

3. Ages of limestone clasts and megaclasts

For many years the assumption was implicit, if not in fact explicit, in most published works on the Middle Palaeozoic of east-central Victoria, that there was no great spread of age represented by the limestones of the Tyers–Boola area and the limestone clasts and megaclasts in the 'basal beds of the Walhalla Group'. Following Philip's (1965) paper on the Tyers conodonts, all were assumed to be more or less *sulcatus* Zone. Additionally, it was suggested that there was in fact 'a lateral facies

change between the Wilson Creek Shale and the Coopers Creek Limestone' (VandenBerg 1988, p. 115).

Samples from the Evans Brother's Quarry limestone megaclast (loc. 16) have produced, *inter alia*, two specimens of *Eognathodus sulcatus* lambda morph, one from our sampling, one from Cooper's (1971) sampling. These indicate that this particular megaclast is no older than *kindlei* Zone. As the megaclast must have been lithified before incorporation into the base of the Wilson Creek Shale, the age of the megaclast provides a maximum age of *kindlei* Zone for the base of the Wilson Creek Shale, at least a whole zone younger than was previously assumed (VandenBerg 1988, p. 115).

Ozarkodina remscheidensis remscheidensis, a rather long-ranging form not always easily identified, has already been reported (Pickett in Holloway 1991) from a mixed sample from Marble Creek and Middle Crossing, Deep Creek (locs 3–6). We have confirmed its presence in allochthonous blocks at our localities 3, 6 and 17. A tabular clast of crinoidal limestone from the Middle Crossing, Deep Creek, locality 3 (our sample 3A), produced *O. remscheidensis remscheidensis* in association with ?*O. steinhornensis eosteinhornensis, O. excavata excavata*, and *O. confluens*. If presence of the last two species could be confirmed there would be evidence for a Pridoli (latest Silurian) age and evidence for carbonate sedimentation having commenced appreciably earlier in this part of Victoria than was indicated in recent syntheses (VandenBerg & Garratt 1976; VandenBerg 1988). Even so, caution would still be necessary as there is imprecision regarding time-ranges of these and closely related forms.

High precision eludes us regarding correlation of the other Marble Creek, Deep Creek and most of the Coopers Creek limestone clasts and megaclasts, largely because of the high proportion of barren samples, and the generally low yields and low diversities obtained from others (Table 2). Subjectively, the faunas obtained from the clasts and megaclasts appear to be slightly older than *sulcatus* Zone, but there is no compelling evidence. The presence of *Pand. optima* at localities 4W, 17 and 18 and *Pand. remscheidensis repetitor* at Loc. 19 indicate those blocks to be no older than *postwoschmidti* Zone. The fauna from Loc. 4W includes a specimen regarded by us as best referred to *Erika* (Fig. 14K), a genus known only from horizons of *delta* age, but additional material is needed to confirm this identification. The presence of *O. r. remscheidensis* in clasts 3A, 6, and 17 seems to indicate little possibility that they could be younger than *sulcatus* Zone.

4. The autochthonous carbonate units at Waratah Bay

The Waratah and Bell Point limestones of Waratah Bay, about 90 km south-southwest of Tyers (Fig. 5), are approximately the same age as the Tyers–Boola carbonate fan and the limestone megaclasts of the southern Walhalla Synclinorium. Because we believe the Waratah Bay sequences to have relevance for reconstructing the Devonian palaeogeography of east-central Victoria during Devonian times, it is appropriate to reevaluate the age of these units. Reference should be made

Fig. 5.   Cartoon illustrating palaeogeographic relationships in west Gippsland in mid Early Devonian times, assuming gross relationship of main crustal blocks was the same as at present. This, conceivably, may not have been so.

to papers by Talent (1965, 1989), Argent (1971), Bischoff and Argent (1990) and Mawson et al. (1992) for discussion of the stratigraphy, structural setting and conodont faunas from these units. Of Argent's samples, 36 produced forms of *Eognathodus*; most others yielded forms of no great correlative significance, and numerous samples were barren. We have already (Mawson et al. 1992, p. 39) rejected the identification of *Polygnathus pireneae* from Argent's sample 163 from Teichert's (1954) Bluff Member and, by implication, evidence for identifying latest Pragian (*pireneae* Zone) at Waratah Bay. We also pointed out the danger of inferring a Lochkovian (*pesavis* Zone) interval in the lower part of the Waratah Limestone on the basis of absence of critical forms.

In inferring a *pesavis* age from what they termed the 'Lower Grinder Member' and the 'Mushroom Rock Member' of the Waratah Limestone, Bischoff & Argent (1990) based their opinion on the presence of *Pand. exigua philipi* in their sampled sections. In support of this judgment they incorrectly quoted Savage's (1977) paper on Early Devonian conodonts from the Karheen Formation of Alaska, stating that in 'material from Alaska where *P. exigua philipi* occurs together with *Kimognathus alexeii* Mashkova in the *pesavis* Zone' (Bischoff & Argent 1990: 459). In fact Savage provided data on only two localities in the Karheen Formation, both of which yielded specimens of *Pand. exigua philipi* together with *Eognathodus sulcatus* but neither of which produced specimens of *K. alexeii*. Bischoff & Argent (1990: 459) quote Savage & Gehrels (1984) as support for co-occurrence of *K. alexeii* and *Pand. e. philipi* being suggestive of 'a late *pesavis* or early *sulcatus* Zone age'. Likewise, their unreferenced report from the Garra Formation of the occurrence of *Pand. e. philipi* from within the *pesavis* Zone is not firm evidence for the lower part of the Waratah Limestone being necessarily referable to the *pesavis* Zone. In fact, the co-occurrence of *Ozarkodina eberleini* with *Pand. e. philipi* is more suggestive of assignment to the *sulcatus* Zone (Savage 1977; Klapper & Johnson 1980; Savage & Gehrels 1984).

At Grinder Point, the first forms referred to *Eognathodus sulcatus* were obtained by Bischoff & Argent (1990) from 109 m above the unconformity at the base of the Waratah Limestone (Talent 1989; Mawson et al. 1992). The interval 0–109 m was assigned by them to the *pesavis* Zone but none of the taxa in the low-diversity assemblage obtained from this interval necessarily suggests a pre-*sulcatus* age. The basal section of Waratah Limestone resting unconformably on dolomites of the Digger Island Formation west of Robins' Rocks
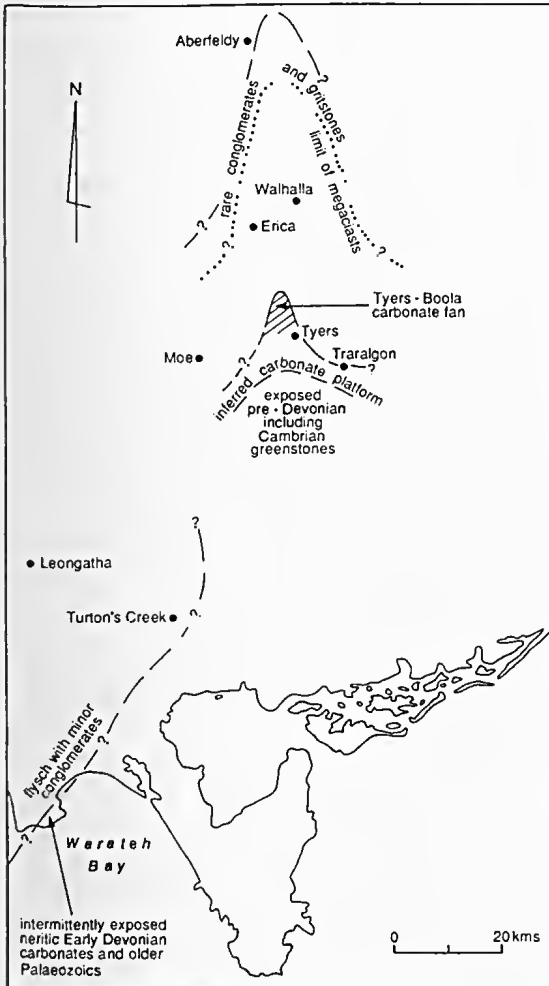
on the shoreline (= 'Black Stack' of Bischoff &
Argent) likewise failed to yield unequivocally pre-
Pragian conodonts; we have sampled a section
at Robins' Rocks with similar equivocal results.
Bischoff and Argent's sections at Gair Rock and
Mushroom Rock produced *E. sulcatus* in the
stratigraphically lowest horizons sampled but both
sections commence stratigraphically well above the
lowest horizon to yield *E. sulcatus* at Grinder Point
(?*c*. 20 m in the case of their Mushroom Rock
section; ?*c*. 35 m in the case of their Gair Rock
section). We therefore find no compelling evidence
for or against horizons referable to the *pesavis*
Zone at Waratah Bay.

The forms of *E. sulcatus* illustrated by Bischoff
& Argent (1990) from the Waratah Limestone and
the Bell Point Limestone at Waratah Bay were
assigned to three of the morphs discriminated by
Murphy et al. (1981): their iota, kappa and mu
morphs. Few illustrations were given of the critical
undersides of most specimens figured. In fact, the
only illustration (Bischoff & Argent, 1990, pl. 3,
fig. 1) of the lower surface of a specimen identified
as *E. sulcatus* mu morph from Bell Point 71, the
species critical for discriminating *kindlei* Zone, is
almost identical to the lower surface of a specimen
identified as *E. sulcatus* kappa morph from Gair
Rock 19 (Bischoff & Argent, 1990, pl. 3, fig. 8).
Until adequate documentation has been presented
for other specimens identified as *E. sulcatus* mu
morph, there is no compelling conodont evidence
to indicate an age other than *sulcatus* Zone for
either the Waratah or Bell Point limestones. Until
such data become available, one must continue to
rely on the incompletely documented macrofossil
faunas of these units.

5. *Implications regarding palaeogeography*

All limestone bodies interpreted by us (see above)
as megaclasts occur in the southern part of the
Walhalla Synclinorium. Apart from the Loyola
occurrences (Cooper 1973a; Mawson et al. 1992)
c. 90 km north of Walhalla, no limestone clasts
of substantial size occur farther north than loc. 27,
about 15 km north-northwest of Walhalla. The
general pattern of decreasing grain size of the
conglomerates northwards from Tyers through the
Coopers Creek and Walhalla regions, the evidence
for exposed Cambrian greenstones shedding det-
ritus into the same region (Junner 1915; Thomas
1942; VandenBerg 1988), and the presence of a
large carbonate fan in the Tyers–Boola area are
all consistent with existence of a land area with
a carbonate platform or platforms somewhere to
the south of the Tyers–Boola area (VandenBerg

1988; Webb 1991) during Early Devonian times
(Fig. 5). We consider the richly fossiliferous lime-
stone megaclasts to have been dislodged from this
'lost' carbonate platform or platforms and thus to
provide evidence for a portion of the spectrum of
carbonate lithologies that were formerly repre-
sented. The range of ages indicated by the Tyers–
Boola carbonate fan and by the limestone mega-
clasts is consistent with persistence of carbonate
sedimentation around this landmass during the
interval from late Lochkovian through the Pragian
until at least earliest Emsian times, with carbonate
sedimentation having possibly commenced in
the latest Silurian (Pridoli). The autochthonous
shallow water Early Devonian limestones in an
intermittently emergent area at Waratah Bay, dis-
cussed below, may have formed part of the same
platform or been part of another platform.

The spectrum of lithologies represented by
the limestone boulders and megaclasts from the
Platina–Coopers Creek and Deep Creek–Marble
Creek areas ranges from crinoidal limestones
to limestones rich in algae, tabulate corals and
stromatoporoids. Apart from a peculiar dolomitic
arenite present in clasts and megaclasts at locality 1,
we have not noted very shallow marine lithologies
such as poorly fossiliferous dolomitic limestones,
algal pisolites, or calcarenites and calcisiltites with
notably low diversity brachiopod and/or bivalve
faunas like those of the latest Pragian–earliest
Emsian Buchan Caves Limestone to the east (Talent
1956a; Mawson et al. 1992). Nor are there lith-
ologies such as dolomitic stromatoporoid-tabulate
coral-rugosan-rich or mollusk-rich limestones cor-
responding to the very shallow water Pragian
Lilydale Limestone to the west. It thus seems that,
in general, the collapse structures responsible for
the debris flows and megaclasts in the Boola,
Wilson Creek and Norton Gully formations in the
southern Walhalla Synclinorium did not bite into
the adjacent Pridoli–Pragian carbonate platform
margin with sufficient depth to supply a complete
spectrum of the carbonate lithologies formerly
represented around the platform.

Talent (1965) suggested that the makeup of the
macro-fauna obtained from debris flows in the
Liptrap Formation at Waratah Bay and from the
coastline west of Cape Liptrap was consistent with
derivation during late Early Devonian time from
exposed Waratah Limestone. In the absence of
identifiable material derived from a Bell Point
Limestone source, he argued for slotting the
Liptrap Formation into the erosional gap between
the Waratah and Bell Point limestones; he had
assumed no major lateral displacement along the
Walkerville Fault. VandenBerg (1975, 1988, in

VandenBerg & Garratt 1976), by a sedimentologic argument but without constraining evidence as to age, asserted that the Liptrap Formation should be regarded as postdating the Bell Point Limestone. He rejected alignment of the Liptrap Formation with the Boola Formation [= Coopers Creek Formation of VandenBerg & Garratt 1976, p. 57], preferring to align it with the Norton Gully Sandstone. The history of movements along the Walkerville Fault still needs to be chronicled; the scale of translation between the blocks to east and west of it is not known. It is possible that juxtaposition of the tract of Liptrap Formation against the Cambrian–Devonian sequence of the 'Waratah Axis' could be an artifact of post–Early Devonian tectonics. It is also conceivable that the limestone cobbles (and their faunas) found in slumps in the Liptrap Formation were derived from a source other the Waratah Limestone or some former extension of it. Thus the precise age of the Liptrap Formation and its palaeogeographic situation during Early Devonian times need clarification.

6. Boulder Flat: a footnote

In dealing with the metamorphosed conodonts from Boulder Flat, eastern Victoria (Mawson et al. 1992), we drew attention to two forms we believed to be early polygnathids, *Polygnathus trilinearis*, of which we had 15 specimens, and a much narrower form of which we had only 5 specimens and which we identified as *P.* cf. *pireneae*. Material from the Tyers–Boola area demonstrates that the two forms from Boulder Flat had independent ancestry, the first being probably derived from *Eognathodus sulcatus* lambda morph, a wide form, and the second form, *E. sulcatus* mu morph, a narrow form. The lineages thus go back to at least the beginning of the *kindlei* Zone, predating development of '*Polygnathus*' discriminated from *Eognathodus* by a median carina.

EVOLUTION OF *EOGNATHODUS* AND *POLYGNATHUS*

From his studies of the conodonts from the old Tyers Limestone Quarry, Philip (1965) suggested *Eognathodus* to be derived from 'spathognathodid' (= ozarkodinan) stock. Based on the degree of constriction of the basal cavity, Klapper (1969) identified two forms of '*Spathognathodus*' *sulcatus* in faunas from Royal Creek, Nevada: an early form with a large, open basal cavity and a late form with a more restricted basal cavity. Additionally, he recognized morphological similarity between '*S.*' *sulcatus* and a younger species, '*S.*' *linearis*

described by Philip from faunas from Buchan, Victoria, from what was later to be found to be a sequence spanning the *dehiscens* to *serotinus* zones (Mawson, 1987a). According to Murphy et al. (1981: 753), Klapper subsequently noted that, despite some similarity to '*S.*' *linearis*, that the forerunner to '*S.*' *sulcatus* was probably '*S.*' cf. '*S.*' *linearis* from Ikes Canyon, Nevada. It was shown to occur with *Pedavis pesavis* in samples from 136 m above the base of the McMonnigal Limestone (Klapper, 1977, fig. 4) and was subsequently illustrated as *Ozarkodina 'linearis'* (Philip) *sensu* Klapper (1977) (= *Ozarkodina pandora* Murphy et al. 1981).

Argument for the *Eognathodus* lineage arising from *Ozarkodina pandora* via a series of morphotypes (Murphy et al. 1981; Weddige 1987; Murphy 1989) is compelling. Evolution from *E. sulcatus eosulcatus* (= eta morph) to *E. sulcatus sulcatus* to *E. sulcatus juliae* (= kappa morph) to *E. sulcatus kindlei* (= lambda and mu morphs) has been carefully demonstrated (Lane & Ormiston 1979; Murphy et al. 1981). The last of this lineage, *E. sulcatus kindlei* is known to persist into and extend to close to the top of the *pireneae* Zone (Lane & Ormiston 1979).

In the collections from the Tyers and Boola quarries, *E. sulcatus* appears to be represented by two populations, one consisting of narrow forms and the other of wide forms. The narrow form of *E. sulcatus* tends to retain the 'normal' ornamentation of a parallel row of nodes on the upper surface whilst the ornamentation of the wide form can take on a variety of forms: two parallel rows of nodes, a ladder-like arrangement of horizontal ridges, an irregular arrangement of nodes on either side of a sulcus, or an irregular arrangement of nodes without a sulcus. In the wide form, the reduction in size of the basal cavity is less pronounced than in the narrow forms because of the geometry involved.

In a study of Early Devonian conodonts from Boulder Flat, Victoria, Mawson et al. (1992) argued that *Spathognathodus trilinearis* first described by Cooper (1973a) and later placed in the genus *Eognathodus* (Klapper & Johnson 1975), should be referred to the genus *Polygnathus*. Occurring in their faunas with *P. trilinearis* were five polygnathid specimens identified as *P.* cf. *pireneae*; these were noted as being very narrow forms. It would appear that these narrow polygnathids, giving rise to the *pireneae-dehiscens-nothoperbonus-inversus-serotinus* lineage, probably evolved from the narrow forms of *Eognathodus*. It is also likely that the wide forms of *Eognathodus* may have given rise to the *P. trilinearis-abyssus-*

perbonus–labiosus–pseudoserotinus lineage. This would imply that the subspecies of *P. dehiscens* proposed by Mawson (1987a) as *P. dehiscens abyssus* should, in fact, be regarded as a separate species, i.e. *P. abyssus*.

It appeared puzzling that the genus *Eognathodus* should not be represented in the interval from the *pireneae* Zone until reappearance in the *costatus* Zone (e.g. Klapper & Johnson 1980; Mawson & Talent, 1989) with the incoming of the widely reported species *E. bipennatus* (Bischoff & Ziegler). It is now argued (Mawson 1993) that the derivation of *E. bipennatus* was not from the Early Devonian eognathodid lineage but from another lineage of ozarkodinans, through *Pand. palethorpei* (Telford 1975), a species yet to be reported from the Northern Hemisphere.

SYSTEMATIC PALAEONTOLOGY

As the majority of conodonts in this study have been documented in the Catalogue of Conodonts (Ziegler 1973, 1975, 1977, 1981, 1991) or described more fully in earlier papers (e.g. Philip 1965; Wilson 1989; Mawson et al. 1992), we have, except for a single instance (*Eognathodus sulcatus* nu morph), limited our documentation to illustrations and discussion, restricting the latter to cases where study of the faunas has provided new information. Type and figured specimens are housed in the palaeontological collections of the Museum of Victoria (NMV P). Precise horizon and locality data for each sample number can be obtained by reference to Figs 6–15 and Tables 1–4.

Genus Pedavis Klapper & Philip, 1971

Type species.   Icriodus pesavis Bischoff & Sannemann, 1958.

Discussion.   Although *Pedavis latialata*, the oldest known species of *Pedavis* from the late Ludlow (Late Silurian, *latialata* Zone), and *Ped. pesavis* from the late Lochkovian (Early Devonian, *pesavis* Zone) have long been recognized as zonal forms, the biostratigraphic potential of other species of *Pedavis* was not appreciated until Murphy & Matti (1983) elucidated details of the pattern of evolution of *Pedavis*, based on Early Devonian faunas from Nevada. After erecting three new species, *Ped. biexoramus, Ped. breviramus,* and *Ped. brevicauda,* they hypothesized relationships for the various species of *Pedavis* then known, from *Ped. latialata* [*latialata* Zone] to *Ped. mariannae* [*kindlei* Zone] (Murphy & Matti 1983, text fig. 9). *Ped. sherryae* Lane & Ormiston from the *dehiscens* Zone is the youngest representative of the genus.

Metres above base of section 'BOO'	Sample numbers	eta morph	theta morph	iota morph	kappa morph	lambda morph	mu morph	nu morph	incomplete specimens
53.8	Top			1					
52.3	73					1			1
52.1	72			5			7		4
50.3	70				2				
37.3	49	1				1			1
36.8	48	1				1		1	
36.1	47								2
34.8	45				2		1	1	1
34.1	43.7					1	1		
31.2	40					1			
21.9	23	1	4			2			2
21	21			2		1		1	
20.2	20.1						1		
18.8	18.6				1		3		1
17.3	17.1					1		1	
16.8	16.5			5	2	1	5	2	8
16.2	16			3	1	1		3	6
15.3	15			2		2			3
14.8	14.5			2	1	1			3
14.1	13.8		3	14	1	3	1		4
13.3	13.1							3	
12.2	11.8			1					
11.4	11.1	2		10	1			1	
10.6	10.2						1		
8.3	7.9	1	4	1	2		1		2
8.2	7.8	4	2	10	6	1		1	8
6.7	6.2	3	2	1			4		3
5.8	5.3	2	3				5		1
5.2	4.8	4	1					1	
4.2	3.8	4	1						
3.3	2.8	4	1		1			1	
2.4	2.6			2				1	
1.9	1.8	1	2						
1.4	1.4		1						
1	1	2	3					1	
0.2	0.2				1				

Table 3. Distribution of *Eognathodus sulcatus* morphotypes (*sensu* Murphy *et al.* 1981) through the Coopers Creek Limestone in the BOO section at Boola Quarry.

Metres above base of section 'TQ'	1	2-2.1	2.5-2.7	2.9	3.3	3.5-3.65	4.7-4.8	5	6	6.4-6.5	6.6-6.7	6.8-6.9	7.3	7.7-7.9	9.1	11	11.8-11.9	12.2	14
eta morph									6	3					1		3		
theta morph	2						2	1		1	2	2	1		2	1	7	4	6
iota morph	1		4		1	1	1		3			2	2	3	6		4	4	2
kappa morph	1	1		1											1		1		
lambda morph													1		3		4	3	5
nu morph															6		2	1	1
incomplete specimens		2	1					1	3	5	2			1	9	1	9	6	4

Table 4. Distribution of *Eognathodus sulcatus* morphotypes (*sensu* Murphy *et al.* 1981) through the Coopers Creek Limestone in the TQ section at Tyers Quarry.

Pedavis brevicauda Murphy & Matti

Fig. 6A–K

For synonymy see Murphy & Matti (1983).
Pedavis sp. cf. *Ped. sherryae* Lane & Ormiston. — Uyeno 1991: pl. 2, fig. 18.

Discussion. The illustrated specimens of *Ped. brevicauda* from central Nevada (Murphy & Matti, 1983, pl. 6, figs 14, 16, 17) show the angle formed by the lateral processes with the spindle to vary from 65° to 80°; for the holotype this angle is 70°. Specimens from the BOO section show a slightly greater variation: 63° to 91°. This range of variation can be illustrated with specimens recovered from one bed within the limestone at Boola Quarry, namely in BOO13.8 (Fig. 6A, D, G).

Although Murphy & Matti (1983) show the range of *Ped. brevicauda* to extend almost to the top of the *sulcatus* Zone (Murphy & Matti 1983, text fig. 9), material from the new collections from the Tyers and Boola quarries indicate it occurs in samples with *E. sulcatus* lambda and mu morphs indicative of the *kindlei* Zone. Similarly, the specimen of *Ped. brevicauda* from Solo Creek, Yukon Territory, illustrated by Fåhraeus (1971, pl. 78, figs 1–2) from his sample V-2, occurs in association with several specimens of *Eognathodus sulcatus kindlei* Lane & Ormiston (= *E. sulcatus* lambda morph of Murphy et al. 1981), further confirmation that the upper range of *Ped. brevicauda* is no lower than the *kindlei* Zone.

The specimen illustrated by Uyeno (1991) as *Pedavis* sp. cf. *sherryae* from the Michelle Formation in northwest Canada is characterized by a short, peg-like posterior process deflected laterally, a feature indicative of *Ped. brevicauda*; the posterior process of *Ped. sherryae* is much longer.

Uyeno's specimen occurs with *Polygnathus dehiscens* and *Pand. steinhornensis miae* thus further extending the known range of *Ped. brevicauda* into the *dehiscens* Zone.

Genus Icriodus Branson & Mehl 1938

Type species. *Icriodus expansus* Branson & Mehl, 1938.

Discussion. The dearth of icriodontan elements in Early and Middle Devonian conodont faunas from eastern Australia has been discussed elsewhere (e.g. Mawson 1986, 1987a, 1987b; Mawson et al. 1988, Mawson & Talent 1989). Faunas from Tyers and Boola conform to this general pattern; only seven icriodontan elements have been recovered from the many limestone samples processed for this paper. Philip (1965) recovered just one specimen from his Tyers collections.

Icriodus steinachensis Al-Rawi eta morph Klapper & Johnson

Fig 9K–N

Icriodus bilatericrescens Ziegler. — Philip 1965: 103, pl. 9, figs 30–31.
Icriodus latericrescens Branson & Mehl. — Klapper & Philip 1971: fig. 8.
Icriodus steinachensis n. sp. Al-Rawi 1977: 55–56, pl. 5, figs 42–43.
Icriodus steinachensis Al-Rawi eta morphotype. — Klapper & Johnson 1980: pl. 2, figs 25–27.
Icriodus steinachensis Al-Rawi eta morph Klapper & Johnson. — Murphy & Matti 1983: 58–59, pl. 5, fig. 36.
Icriodus steinachensis Al-Rawi eta morphotype. — Chlupac et al. 1985: pl. 2, figs 13–16.
Icriodus steinachensis Al-Rawi eta morphotype. — Schönlaub 1985: pl. 3, fig. 3.
Icriodus steinachensis Al-Rawi. — Mawson et al. 1988: table 7.
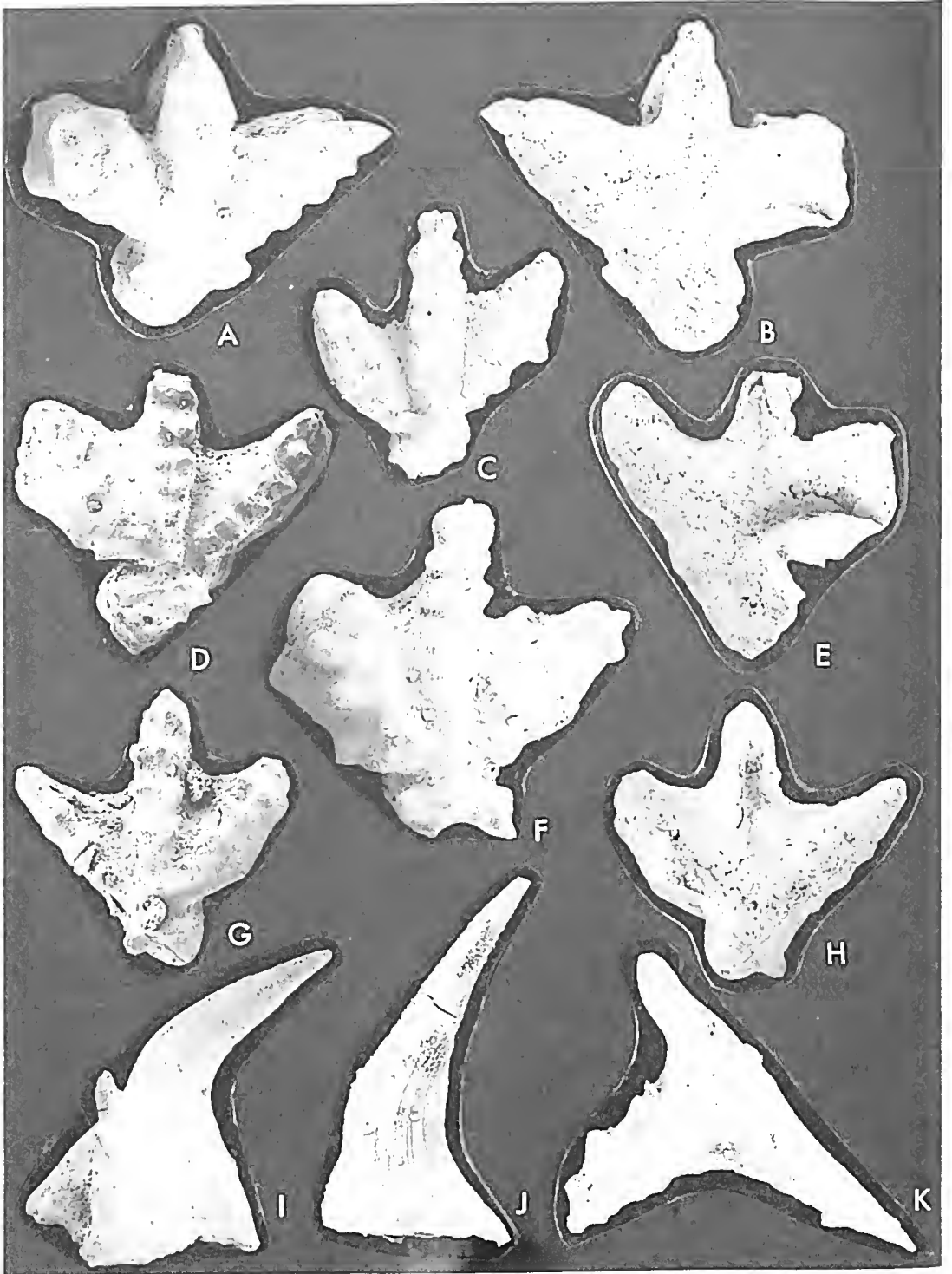
Discussion. As pointed out by Klapper & Johnson (1980: 407) and Murphy and Matti (1983: 58–59), the position of the widest part of the spindle of *I. steinachensis* enables discrimination of two morphotypes: eta and beta. Specimens from the Boola and Tyers quarries (herein and Philip 1965) are assigned to the eta morph because of the typical lenticular outline of the spindle with the widest part of the spindle placed centrally, and the angle of the posterior lateral process to the spindle falling within the range of 'less than 90° to 110°'. Although Klapper & Johnson (1980) indicate *I. steinachensis* eta morph to be restricted to the *pesavis* Zone and *I. steinachensis* beta morph to range through the *sulcatus* and *kindlei* zones, subsequent work on central Nevada material by Murphy & Matti (1983) shows the eta morph to appear first in the middle *delta* Zone and occur in relative abundance through to early in the *kindlei* Zone. Similarly, with material from the Lochkovian and Pragian of the Barrandian and the Carnic Alps, Chlupac et al. (1985, fig. 17) show the first appearance of *I. steinachensis* eta morph to precede the incoming of *I. steinachensis* beta morph.

Four specimens of *I. steinachensis* eta morph and two specimens of *E. sulcatus* have been identified from limestones collected and processed by G. Dongal from what is almost certainly an allo-chthonous block on Limestone Creek a tributary of the Pigna Barney River 49 km north-northwest of Gloucester, N.S.W. This is the first report of limestones of Pragian age from the Tamworth Belt. A specimen of *I. steinachensis* has also been reported from Martin's Well, north Queensland (Mawson et al. 1988).

Amydrotaxis Klapper & Murphy, 1980

Type species. *Amydrotaxis johnsoni* (Klapper, 1969).

Discussion. Four species are presently included in this genus: *Amydrotaxis johnsoni* (Klapper), *Amy. sexidentata* (Murphy & Matti), *Amy. corniculans* Mawson, *Amy. druceana* (Pickett). The last is shown to occur in horizons of *kindlei* age in samples from the Boola and Tyers quarries, and in horizons of *pireneae* age in samples from Boulder Flat, Victoria, where it occurs with *P.* cf. *pireneae* and *P. trilinearis*. (Mawson et al. 1992).

The range of the genus is now taken to be from late in the *postwoschmidti* Zone to somewhere within the *pireneae* Zone.

Amydrotaxis druceana (Pickett)

Fig. 10A–N

For synonymy see Pickett (1980).

Amydrotaxis druceana (Pickett 1980). — Bischoff & Argent 1990: 453–454, pl. 1, figs 1–29.

Discussion. Species of *Amydrotaxis* are discriminated primarily on the basis of the Pa element, especially the outline of the basal cavity and the profile of the blade in lateral view (Klapper & Murphy 1980; Pickett 1980; Murphy & Matti 1983; Mawson 1986). *Amy. druceana* with its asymmetrical, widely flaring basal cavity and with its pronounced tendency to fuse the denticles along the blade, appears to be youngest representative of the genus occurring in faunas of *kindlei* age in the Boola and Tyers quarries sections. From faunas derived from the Boomerang Tank Limestone and the Rookery Limestone, members of the Meryula Formation near Cobar, New South Wales, Pickett (1980) discriminated all elements of the *Amy. druceana* apparatus in sequences of *pesavis* age; these he also recognised in faunas described by Druce (1970) from the Garra Limestone now known to be of *pesavis-sulcatus* age (Wilson 1989). Collections from the Boola and Tyers quarries show the species to occur as well in the *sulcatus* and *kindlei* zones. From limestones of *sulcatus* and probable *kindlei* age from Waratah Bay, Victoria, Bischoff & Argent (1990) illustrated various elements of *Amy. druceana*.

Ancyrodelloides Bischoff & Sannemann, 1958

Type species. *Ancyrodelloides trigonicus* Bischoff & Sannemann, 1958.

Original diagnosis (German). 'Compound conodonts consisting of a denticulated free blade and an arrow-shaped platform with two anterior lobes, on which occasionally one further lobe can be developed, and a pointed posterior lobe. The oral surface of the platform is smooth, except for the fixed blade and median carinae on the lobes.

Fig. 6. A–K, *Pedavis brevicauda* Murphy & Matti. A, B, NMV P143030, I element upper and lower views respectively, ×45, BOO13.8. C, NMV Pt43031, I element upper view, ×45, BOO1. D, E, NMV Pt43032, I element upper and lower views respectively, ×45, BOO13.8. F, NMV P143033, I element upper view, ×60, BOO13.8. G, H, NMV P143034, I element upper and lower views respectively, ×45, BOO13.8. I, NMV Pt43035, M_{2b} element lateral view, ×60, BOO72. J, NMV P143036, M_{2c} element lateral view, ×45, BOOtt.t. K, NMV P143037, M_{2a} element, ×75, Loc. 9.
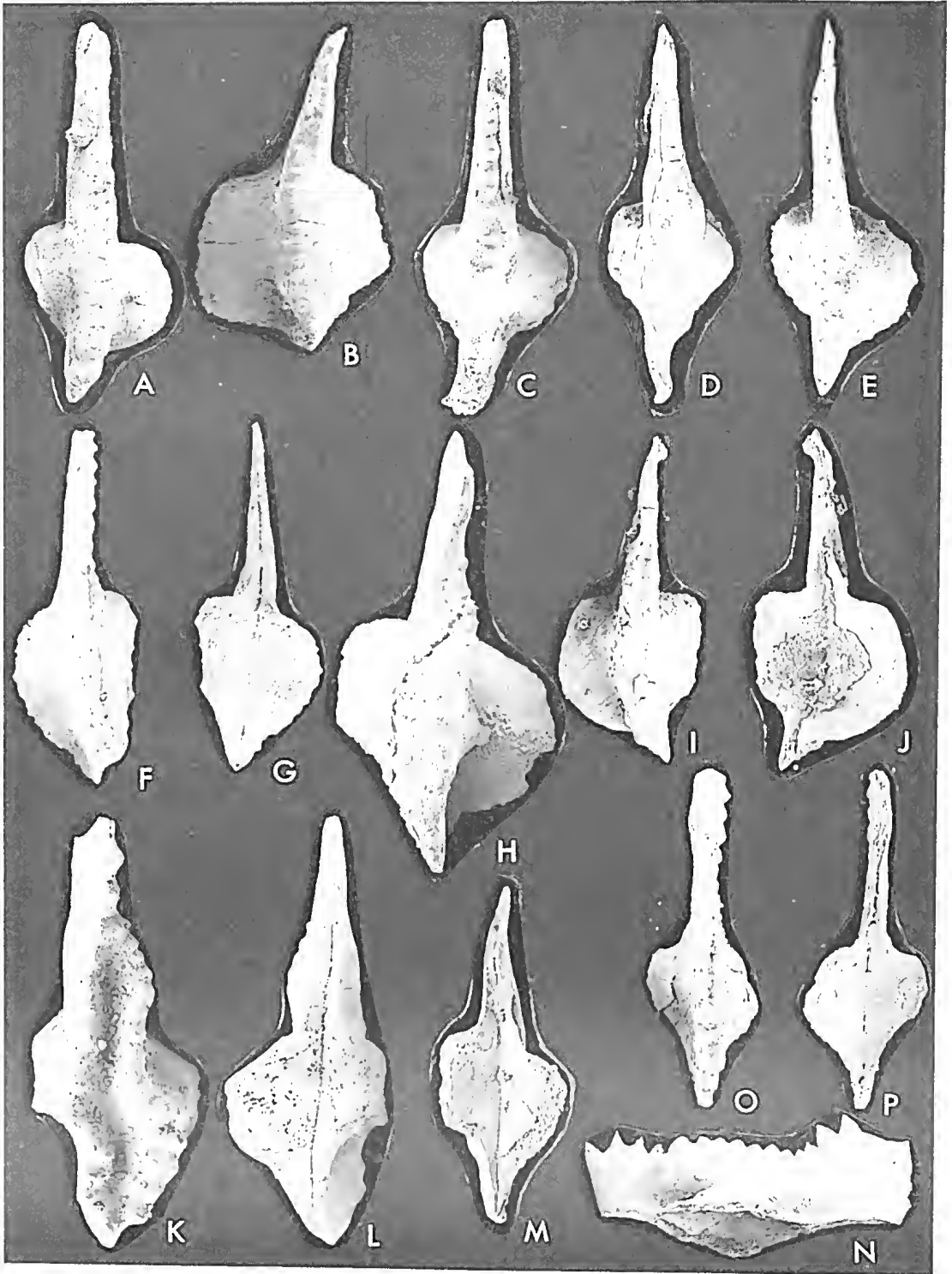
A small basal cavity is on the aboral surface in mature specimens.' (Ziegler 1991)

Amended diagnosis (Murphy and Matti, 1983). 'A polygnathid genus with a well-developed, shelf-like platform, with or without lateral processes and with a basal cavity that is more restricted than the platform *except in the most primitive forms*' (italics ours).

Discussion. Klapper (in Ziegler 1991) accepts Murphy & Matti's (1983) argument that the genus *Ancyrodelloides* evolved from *Ozarkodina remscheidensis* (Murphy & Matti 1983, Figs 3, 4) with the first representative of the genus, *A. omus*, making its appearance late in the *eurekaensis* Zone. New collections from the Tyers and Boola quarries contain large numbers of specimens that are construed as being conspecific with *A. omus*. As they occur in samples with *Eognathodus sulcatus* and *E. s. kindlei* (= lambda and mu morphs), the range of *Ancyrodelloides* is extended from its previously known latest occurrence in the *pesavis* Zone (Klapper, in Ziegler 1991) through the *sulcatus* Zone and into the *kindlei* Zone.

Ancyrodelloides omus Murphy & Matti

For synonymy see Klapper (in Ziegler, 1991).

Discussion. There is some doubt as to generic classification of this species. According to Murphy & Matti (1983), *A. omus* differs from other species of *Ancyrodelloides* in having an unconstricted basal cavity and flattened, shouldered platform lobes that later develop tubercles on the lobes. They argue that, as the genus evolved, the basal cavity of the younger species of *Ancyrodelloides* (Murphy & Matti 1983, text fig. 5) became more constricted and tubercles were developed on the platform shoulders. The grounds Murphy & Matti (1983, p. 13–14) give for referring *A. omus* to *Ancyrodelloides* rather than *Ozarkodina* are fourfold: '1) phylogenetic interpretation of the taxa, 2) the similarity of the basal cavity and groove, 3) the appearance of a distinctive type of (O) element (= Pb element) which is apparently shared by all *Ancyrodelloides* (P) elements (= Pa elements),

and 4) specimens with intermediate morphologies between several of the taxa'. Considering the first and second points, material from Tyers and Boola quarries shows that because of their co-occurrence with numerous specimens of *E. sulcatus* this form, with a wide, open ozarkodinan-type basal cavity, persisted through to at least the *kindlei* Zone. Strangely, no distinctive Pb elements with expanded basal cavity and shouldered blade have been recovered from the Victorian faunas. The few specimens recovered from the Copenhagen Canyon sections, central Nevada, that are intermediate between *O. remscheidensis, A. omus* alpha and *A. omus* beta were not illustrated (Murphy & Matti 1983); no comparison can therefore be made. It could be that this species, with its open basal cavity, is either a persistent primitive feature of *Ancyrodelloides* or that the species might be better placed in *Ozarkodina*.

The stratigraphic range of *O. omus* is not well known. Murphy & Matti (1983) considered its occurrence in Nevada (Murphy & Matti 1983), Germany (Bischoff & Sannemann 1958) and Spain (Bultynck 1971) and showed *O. omus* alpha morph to make its first appearance at the base of the *delta* Zone with *O. omus* beta appearing slightly higher in the section; neither extends into the middle of the *delta* Zone (Murphy & Matti 1983, text fig. 4). Chlupac et al. (1985, fig. 17) indicated that *A. omus* first appeared in the late early Lochkovian and ranged through to early late Pragian in conodont faunas from the Barrandian and the Carnic Alps. Klapper & Johnson (1980) included some specimens illustrated by Philip (1965, pl. 10, figs 5–7) in *O. carlsi* Boersma. In Vol. V of the Catalogue of Conodonts, these were transferred to *Anc. omus* (Klapper in Ziegler 1991). If this re-assignment is accepted, *Anc. omus* has a stratigraphic range from the *delta* Zone into the *kindlei* Zone and the range of the genus *Ancyrodelloides* is from highest *eurekaensis/postwoschmidti* Zone at least to somewhere within the *kindlei* Zone.

Murphy & Matti (1983) differentiated two morphs of *A. omus*: an alpha morph with smooth platform lobes and a beta morph with a tubercle on the platform lobes. In the new collections from

---

Fig. 7. A–N, *Eognathodus sulcatus* Philip 1965, all Pa elements. A–C, eta morphs. A, NMV P143038, upper view, ×45, BOO2.8. B, NMV P143039, upper view, ×45, TQ9.1. C, NMV P143040, upper view, ×60, BOO4.8. D, E, theta morphs. D, NMV P143041, upper view, ×30, BOO5.3. E, NMV P143042, upper view, ×45, BOO1.8. F–H iota morphs. F, G, NMV P143043, upper and lower views respectively, ×60, BOO23. H, NMV P143044, upper view, ×45, BOO11.1. I, J, NMV P143045, iota transitional to kappa morph, upper and lower views respectively, ×30, BOO1.4. K–P, kappa morphs. K, L, NMV P143046, upper and lower views respectively, ×45, BOO13.8. M, N, NMV P143047, lower and lateral views respectively, ×45, BOO11.1. O, P, NMV P143048, upper and lower views respectively, ×75, BOO21.
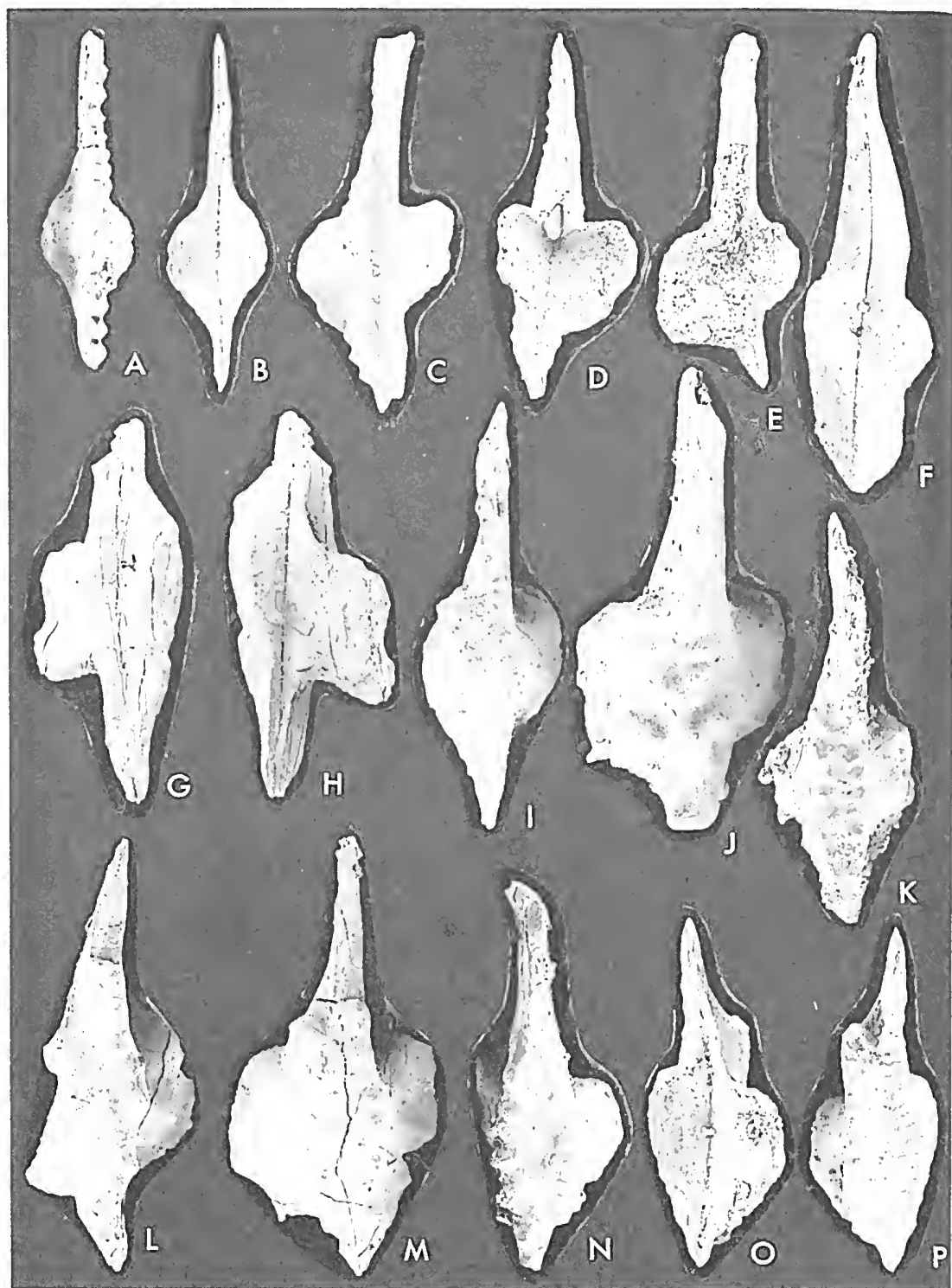
the Coopers Creek Limestone, a number of specimens have been found with a ridge connecting the tubercle to the blade (e.g. Fig. 12F–N); these have been included with the beta morph.

alpha morph

Fig. 11H–L

Discussion. The large number of specimens of *O. omus* with smooth platform lobes showing a tendency, with the onset of maturity, for a thickening or parapet to build up on the upper surface of the platform lobes (Fig. 11H). The parapet is clearly visible in one of the specimens illustrated by Philip (1965, pl. 10, fig. 10).

beta morph

Fig. 12A–N

Discussion. In many specimens from Tyers and Boola quarries, the tubercle on the platform lobe is connected by a ridge to the main row of blade dentticles. Measuring the length of a sample of both populations showed the average length of the 'ridged' specimens to be 1.07 mm compared to 1.24 mm for 'tuberculate' specimens. This may be related to the stage of growth; the 'ridged' form is here considered to fall within beta morph. As the average length of the smooth-lobed specimens is very close to that of 'ridged' specimens, 1.05 mm, it seems unlikely that all smooth-lobed specimens would eventually develop ridges and/or tubercles, particularly as specimens of the smooth-lobed form have been obtained up to 1.5 mm in length.

Genus Eognathodus Philip 1965

Type species. *Eognathodus sulcatus* Philip 1965.

Discussion. At the time of the publication of the Catalogue of Conodonts Part III (Ziegler 1977), this genus included only four species: *E. sulcatus, E. secus, E. bipennatus* and *E. trilinearis.* The last of these, *E. trilinearis* (Cooper 1973a) was recently reassigned to the genus *Polygnathus* (Mawson et al. 1992). Topotype material of *E. sulcatus* and *E. secus* obtained during the present investigation

suggests they are best regarded as synonyms, *E. secus* being most likely a gerontic form of one of the morphs of the highly variable *E. sulcatus.* Elsewhere (Mawson 1993) the species *bipennatus* has been assigned to a new genus.

Eognathodus sulcatus Philip

Figs 7A–N, 8O–P, 9A–1

For synonymy see Murphy, Matti and Walliser 1981.
Eognathodus sulcatus Philip 1965.—Bischoff & Argent 1990: 454–456, pl. 2, figs 1–31, pl. 3, figs 1–13, 15–19.
Polygnathus pireneae Boersma 1974a.—Bischoff & Argent 1990: 459, pl. 3, fig. 14.

Discussion. The conodont fauna from the Tyers limestone quarry, from which *E. sulcatus* was first described, was extracted from a 20 kg bulk sample made up of various lithologies exposed in the quarry (Philip 1965). The specimen chosen by Philip (1965) as the holotype is a large specimen, 1.8 mm in length; other specimens illustrated by him are much smaller: 1.05 mm and 1.2 mm. Few, if indeed any, specimens that can closely be compared with the holotype of *E. sulcatus* have been reported globally, but many that are obviously conspecific with Philip's paratypes of this species are widely distributed (for example, North America: Klapper 1969, Fåhraeus 1971, Klapper 1977, Murphy et al. 1981, Savage 1977, Savage et al. 1977, Savage & Gehrels 1984, Lane & Ormiston 1979, Murphy 1989; Europe: Al-Rawi 1977, Murphy et al. 1981, Schönlaub 1985, Weddige 1987; Asia: Wang et al. 1979). Because justified concern regarding the relative stratigraphic position of the holotype of *E. sulcatus* and its paratypes has been voiced (e.g. Murphy 1989, and at meetings of the Subcommission on Devonian Stratigraphy), systematic bed-by-bed collection of sections at the Tyers and Boola limestone quarries (Fig. 4) was carried out. Over four hundred specimens of the various morphs of *E. sulcatus* were recovered from the two sections (Tables 1 and 2); these are classified according to the morphs of Murphy et al. (1981) (Tables 3 and 4). From study of both the upper and lower surfaces of the specimens, the following observations can be made:

Fig. 8. A–P, *Eognathodus sulcatus* Philip 1965, all Pa elements. A–D, lambda morphs. A, B, NMV P143049, upper and lower views respectively, ×75, BOO13.8. C, D, NMV P143050, upper and lower views respectively, ×30, BOO13.8. E–H, mu morphs. E, NMV P143051, lower view, ×30, TQ7.7–7.9. F, NMV P143052, lower view ×60, BOO73. G, H, NMV P143053, upper and lower views respectively, ×45, BOO20.1. 1, early nu morph, NMV P143054, upper view, ×45, BOO6.2. J–P, nu morphs. J, NMV P143055, upper view, ×45, BOO5.3. K, NMV P143056, upper view, ×30, BOO5.3. L, NMV P143057, upper view, ×45, BOO7.8. M, NMV P143058, upper view, ×45, TQ11.8–11.9. N, NMV P143059, upper view, ×30, BOO48. O, P, NMV P143060, lower and upper views respectively, ×45, BOO13.1.
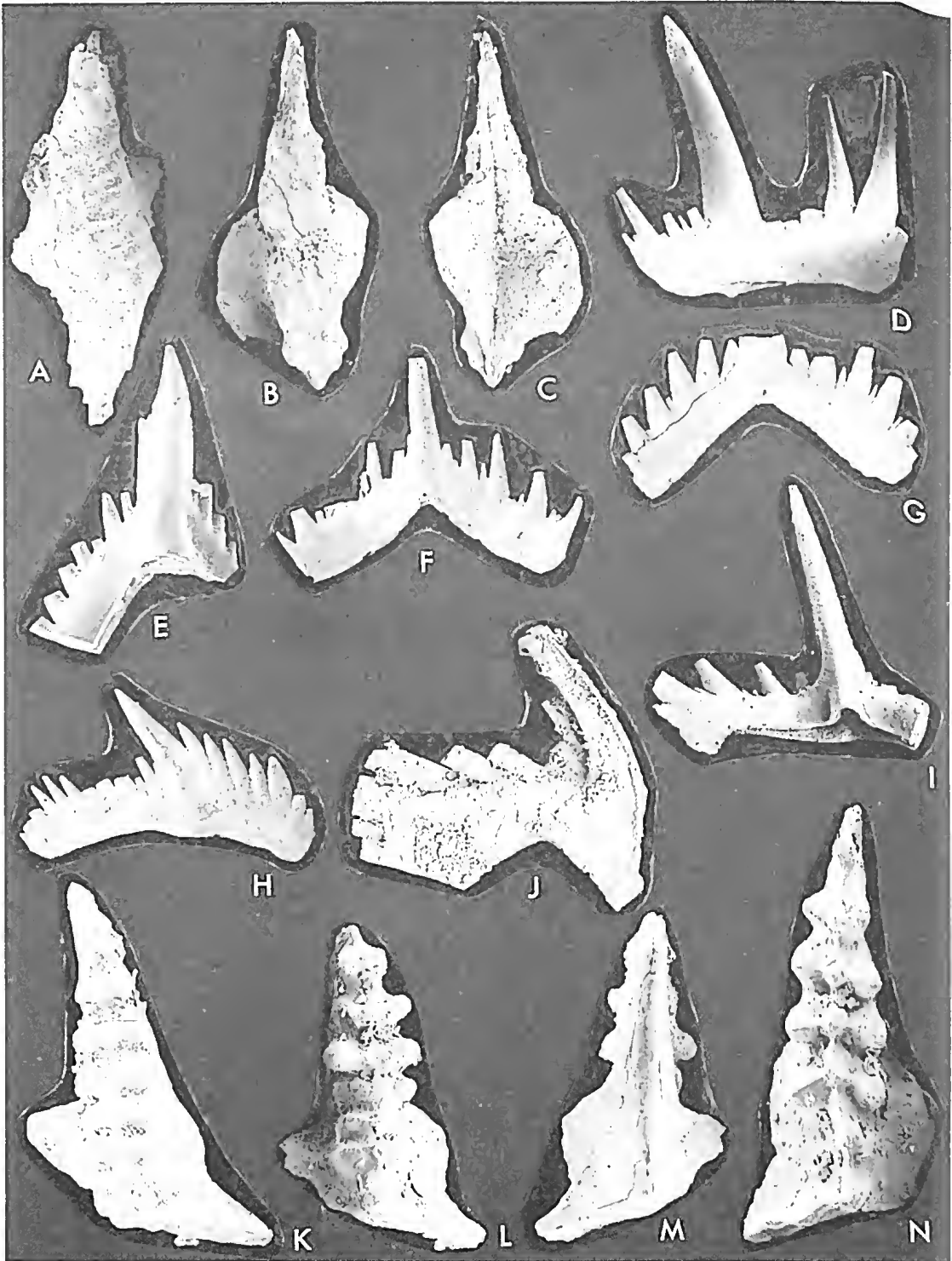
1. The incoming of lambda and mu morphs occurs 7.3 m and 7.8 m above the base of the Tyers and Boola sections respectively; these levels are therefore taken to indicate the base of the *kindlei* Zone.

2. *E. sulcatus* is a very variable species. Murphy et al. (1981) discriminated 6 morphs: eta, theta, iota, kappa, lambda and mu. A seventh morph (herein referred to as the nu morph) makes its entry at 9.1 m and 5.5 m above the base of the Tyers and Boola sections respectively. The new morph is introduced to encompass the novelties of upper surface ornamentation that can be observed in the populations of *E. sulcatus* from the Tyers–Boola area. The two specimens identified by Philip (1965) as *E. secus* are best seen as belonging to this morph (see below) as their irregular upper surface ornamentation comes within its range of variation.

3. Whereas there is a general tendency for the basal cavity of *E. sulcatus* to decrease in size with time: from *E. sulcatus sulcatus* to *E. sulcatus juliae* to *E. sulcatus kindlei*, *sensu* Lane & Ormiston (1979) [or *E. sulcatus* eta to kappa to mu morphs *sensu* Murphy et al. (1981)], the populations appear to contain two main forms: a narrow form and a wide form. The narrow form tends to retain the 'normal' ornamentation of a parallel row of nodes on the upper surface whereas the ornamentation of the wide form can be expressed in various ways (see immediately below).

Eognathodus sulcatus nu morph

P element

Figs 8I-P, 9A–C

Eognathodus secus sp. nov.—Philip 1965: 100–101, pl. 10, figs 22–23.
Eognathodus sp.—Philip 1965: 102, pl. 10, fig. 19.

Diagnosis. The *sulcatus* nu morph is characterized by a relatively wide basal cavity and variable ornamentation of the blade ranging from parallel rows of variably sized nodes, a ladder-like arrangement of horizontal ridges, an irregular arrangement of nodes on either side of a sulcus, or an irregular arrangement of nodes without a sulcus but commonly with nodes in addition to the normal two rows. The *sulcatus* nu morph differs from eta morph in that the denticle pattern extends from the central part of the blade to the posterior end.

Material. 33 specimens from 15 horizons.

Discussion. In the Boola Quarry section, the *E. sulcatus* nu morph appears high in the *sulcatus* Zone, 2.5 m above the first appearance of the *E. sulcatus* lambda morph (base of the *kindlei* Zone). In the Tyers Quarry section, the *E. sulcatus* nu morph first appears just 1.8 m above the base of the *kindlei* Zone. As the Mill Canyon and Rabbit Hill Limestone sections investigated by Murphy et al. (1981) did not extend far into the *kindlei* Zone, it is not surprising that examples of this morph were not encountered there.

Genus **Pandorinellina** Müller & Müller, 1957

Type species. *Pandorina insita* Stauffer, 1940.

Discussion. The distinction between the genera *Pandorinellina* and *Ozarkodina* is made on the basis of the Sa element. The rarity of Sa elements in the faunas from Boola and Tyers quarries makes differentiation of the two problematic; conventional assignment is therefore followed.

Pandorinellina steinhornensis miae (Bultynek)

Fig. 11A–G

Type species. *Spathognathodus steinhornensis miae* Bultynck, 1971.

For synonymy see Klapper & Johnson (1980).

Pandorinellina steinhornensis praeoptima (Mashkova) *sensu* Lane & Ormiston 1979.—Uyeno 1991, pl. 1, fig. 19.

Discussion. The numerous specimens of *Pand. s. miae* from the Tyers and Boola quarries, exhibit the main features documented by Bultynek (1971) from the type locality in the Sierra de Guadarrama, Spain: a restricted asymmetrical basal cavity positioned slightly posterior of centre; curvature of the

Fig. 9. A–I, *Eognathodus sulcatus* Philip 1965. A–C, nu morphs. A, NMV P143061, upper view, ×45, TQ9.1. B, C, NMV P143062, upper and lower views respectively, ×45, TQ9.1. D, NMV PO143063, Se element, lateral view, ×75, BOO3.8. E, NMV P143064, M element, lateral view, ×45, BOO13.1. F, G, Sa elements. F, NMV P143065, lateral view, ×60, Loc. 8. G, NMV P143066, lateral view, ×60, BOO23. H, Pb element, NMV P143067, lateral view, ×45, BOO23. I, Sb element, NMV P143068, lateral view, ×60, BOO/0. J, unassigned Pb element, NMV P143069, lateral view, ×60, TQ6. K–N, *Icriodus steinachensis* Al-Rawi 1977 eta morph Klapper & Johnson 1980, all I elements. K, I, NMV P143070, upper view, ×60, TQ9.1. L, M, NMV P 143071, upper and lower views respectively, ×60, BOO23. N, NMV P143072, upper view, ×90, BOO top.
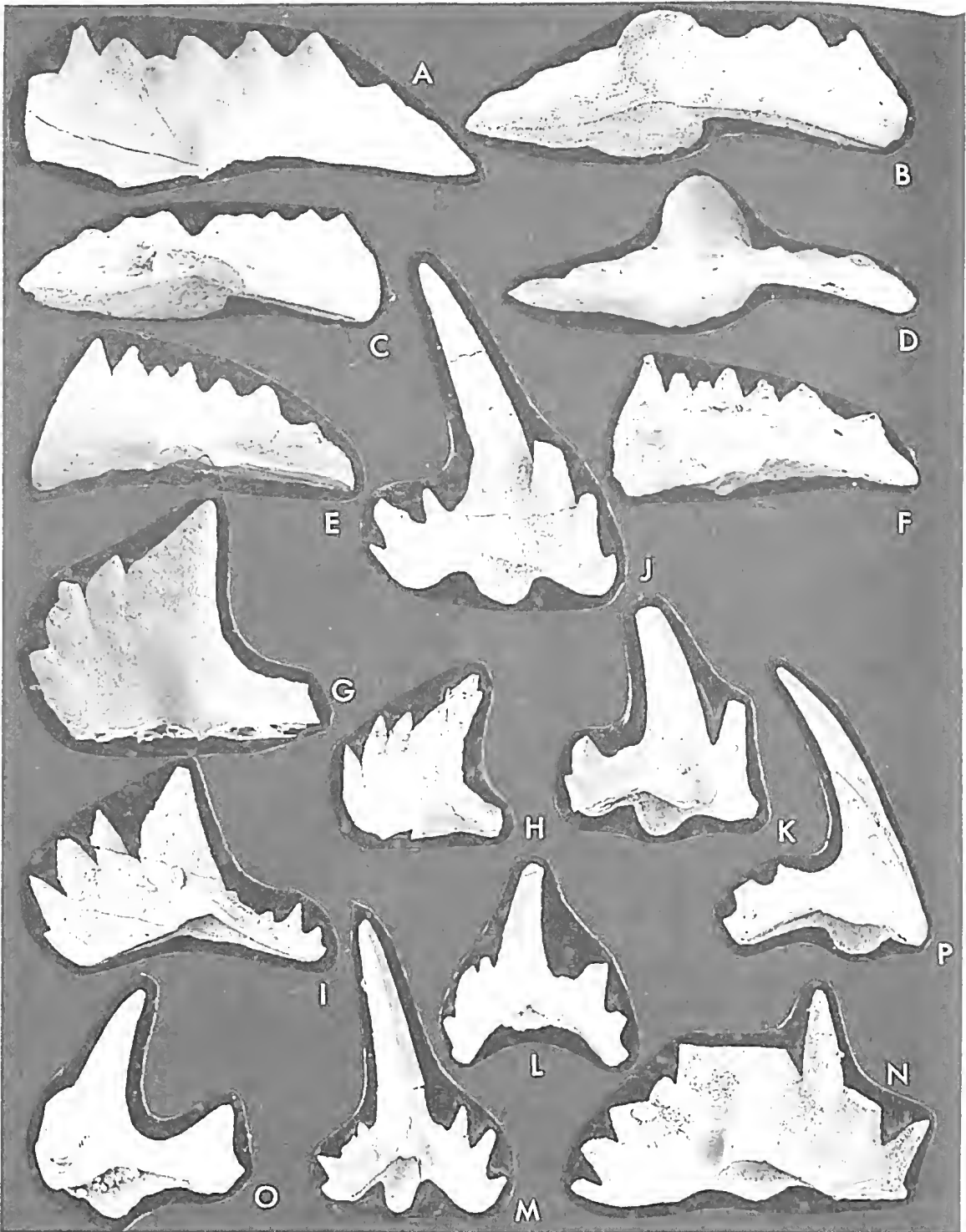
blade posterior of the basal cavity; and triangular denticles arranged with a prominent one above the basal cavity as well as a few prominent denticles towards the anterior of the blade.

Specimens from the type locality, however, are from the *dehiscens* Zone whereas those from the Tyers–Boola area are of *sulcatus-kindlei* age. Most other reports of *Pand. s. miae*, for example from Morocco (Bultynck & Hollard 1980), east-central Alaska (Lane & Ormiston 1979) and Central Asia (Mashkova 1978) are from the *dehiscens* Zone. In the Oberbuchaeh II section in the Carnic Alps (Schönlaub 1985) *Pand. s. miae* makes its appearance prior to the entry of *P. dehiscens* and could possibly have commenced within the *pireneae* Zone.

Genus **Polygnathus** Hinde, 1879

Type species.   *Polygnathus dubius* Hinde, 1879.

Discussion.   For discussion regarding the derivation of the genus via *Eognathodus*, see Klapper & Philip (1972), Klapper & Johnson (1975), Cooper (1973a), and Mawson et al. (1992), and direct from *Ozarkodina* see Lane & Ormiston (1979) and Sweet (1988). Material from the Boola and Tyers quarries strengthens the case for the derivation via *Eognathodus*: two forms of *E. sulcatus*, a narrow and wide form, may have given rise to *P. pireneae* and *P. trilinearis* respectively.

Polygnathus dehiscens dehiscens Philip & Jackson

Fig. 16F–K

For synonymy see Mawson (1987a) and Uyeno (1990).

Polygnathus dehiscens Philip & Jackson. – Yolkin et al. 1989: p. 238, pl. 2, figs 3–4.
Polygnathus dehiscens dehiscens Philip & Jackson. – Uyeno: p. 82–83, pl. 9, figs 1–4; pl. 17, figs 1, 2; pl. 19, figs 1–4.
Polygnathus dehiscens dehiscens Philip & Jackson. – Mawson et al. 1992: fig. 7I–K.

Discussion.   A single specimen of a juvenile *P. dehiscens* was obtained among a sparse fauna from

Loc. 12 from limestones very high in the Coopers Creek Limestone on the left bank of the Tyers River (Fig. 1). With it occurred a specimen of *Ozarkodina pseudomiae*, known to arise in the *pireneae* Zone and occur commonly in faunas of *dehiscens* age (Mawson et al. 1992). The presence of *P. dehiscens* in the fauna from Loc. 12 confirms that carbonate sedimentation continued in the Tyers–Boola area until at least early in the *dehiscens* Zone (cf. Yolkin et al. 1989). Because of some uncertainty voiced to us by a colleague regarding the lower surface of the type specimen of *P. dehiscens*, it was borrowed from the collections of the Geology Department of the University of New England for examination and photography. The micrographs taken by a scanning electron microscope proved that what was thought to be basal filling attached to the under surface of the type, was in fact a moon-shaped breakage in the basal cavity (Fig. 16H, J, K).

LOCALITY REGISTER

BOO – Section in Boola limestone quarry (Figs 1 and 4) sampled June 1986, commencing in what was then the lower quarry, at the conformable boundary between siltstones of the Boola Formation and limestones of the Coopers Creek Limestone. The quarry has been considerably enlarged since 1986.

TQ – Bed-by-bed sampling, January 1992, across the face of the old Tyers limestone quarry commencing with the lowest limestone exposed in a re-entrant beside the access road at the northern end of the quarry (Figs 1 and 4).

Spot localities

1. A debris flow exposed in the bed of the west (right) branch of Deep Creek. This is the occurrence reported by Baragwanath (1925, pp. 23 and 39, note 19) as 'Small lenticles of highly fossiliferous limestone ranging in size from 1 foot by 3 feet to 6 feet by 20 feet' 'associated with conglomerate up

Fig. 10.   A–P, *Amydrotaxis druceana* (Pickett 1980). A–F, All Pa elements. A, NMV P143073, lateral view, ×60, BOO72. B, NMV P143174, lateral view tilted to show basal cavity, ×45, BOO48. C, NMV P143075, lateral view, ×45, BOO28. D, NMV P143076, upper view, ×60, BOO47. E, NMV P143077, lateral view, ×30, TQ/0. F, NMV P143078, lateral view, ×90, BOO18.6. G, H, Pb elements. G, NMV P143079, lateral view, ×60, BOO72. H, NMV P143080, lateral view, ×60, BOO47, I, ?Pb element, NMV P 143081, lateral view, ×60, BOO72, J, L–N, Sa elements. J, NMV P143082, lateral view, ×60, BOO72. L, NMV P143084, lateral view, ×60, BOO72. M, NMV P143085, lateral view, ×60, BOO72. N, NMV P143086, lateral view, ×60, BOO72. K, O, Sb elements. K, NMV P143083, lateral view ×60, BOO18.6. O, NMV P143087, lateral view, ×60, TQ6. P, Sc element, NMV P143088, lateral view, ×45, BOO18.6.
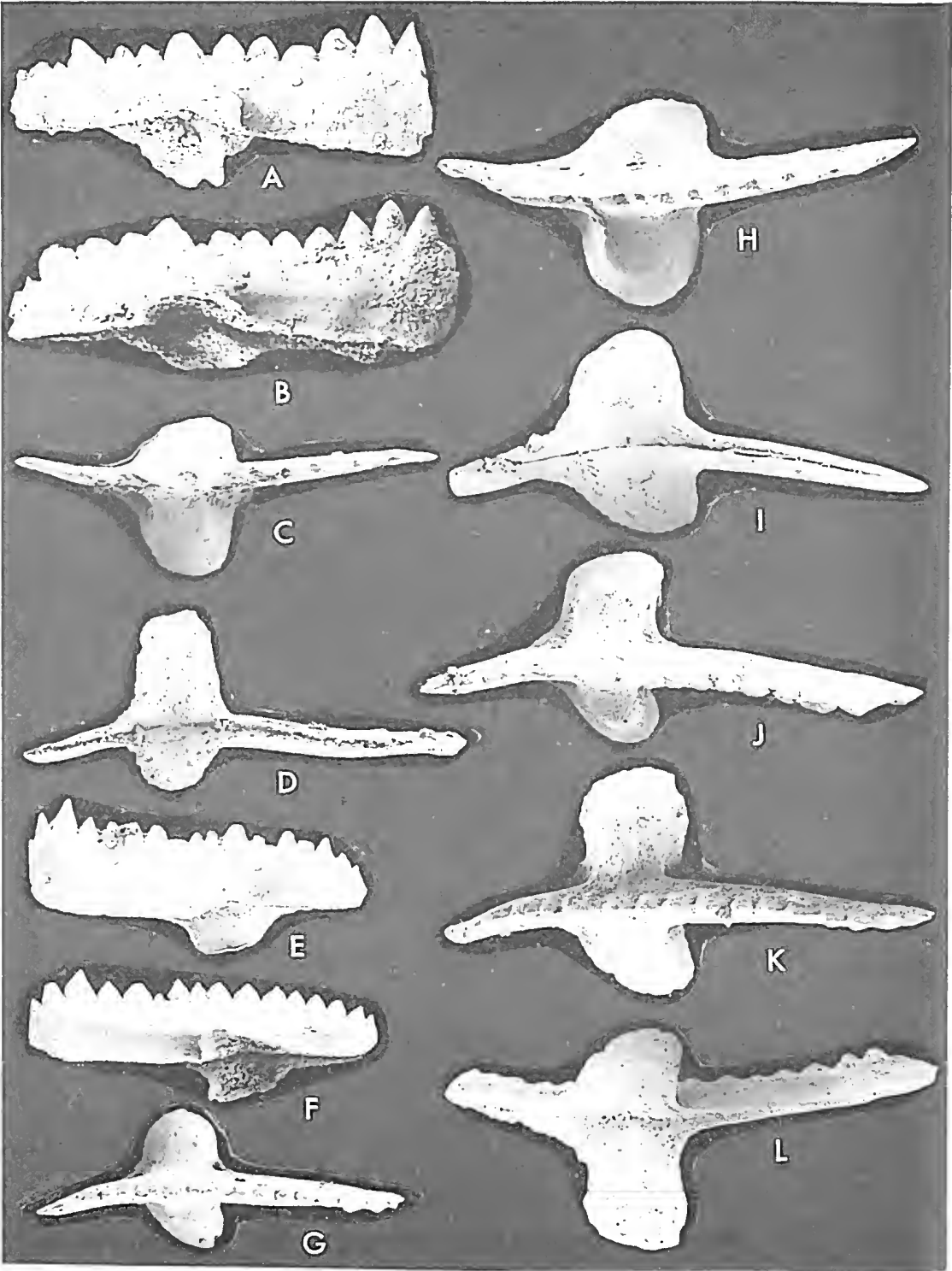
to 12 feet thick, and thin beds of quartzite, chert and slate' on the southern margin of his map of the Aberfeldy district. The locality (Fig. 2, loc. 1), c. 105 m downstream from the crossing of 4-wheel drive road 'Deep Creek No. 2', has numerous cobbles of various lithologies including a fine sandstone with angular quartz clasts 2–3 mm across. We found dolomitic arenite megaclasts but not limestone blocks the size of those noted by Baragwanath in the section exposed in the bed of Deep Creek, obtaining only one prospective, highly crinoidal limestone clast (c. 20 cm across); this produced conodonts, but poorly.

2. Thinly bedded, rhythmically banded, calcareous argillites and argillaceous limestones, lacking macrofossils, outcropping on the right (east) bank of Deep Creek 50–55 m downstream from its junction with Seatabit Creek. This proved barren of conodonts. Several similar occurrences, lacking macrofossils, were noted in Deep Creek and in Seatabit Creek below the Gladstone Track crossing.

3. Immediately east and stratigraphically beneath the limestone body of loc. 4 are sandstones and polymict conglomerates, including limestone clasts up to 0.5 m across, outcropping in the bed of Deep Creek. Samples were taken from a tabular clast of crinoidal limestone c. 2 cm in thickness (loc. 3A), and from a rounded clast c. 30 cm in thickness (loc. 3C).

4. The 'Middle Crossing' Deep Creek limestone body interpreted by us as a megaclast. It is in fact the large body of limestone reported by Baragwanath (1925) as outcropping in Deep Creek '2 miles south' of the southern boundary of his Aberfeldy geological map. The distance given was a misprint; it should have read 5 miles. Samples were taken mid-way up the south flank of the outcrop (loc. 3S) and from the topographically highest point (loc. 3W).

5. Lower 'Toongabbie marble quarry', Marble Creek. Because of discordant relationships to adjacent strata (Kitson 1925), we consider this to be a megaclast.

6. Upper 'Toongabbie marble quarry', Marble Creek. Because of discordant relationships to adjacent strata (Murray 1887, p. 46, 1895, p. 38), we consider this to be a megaclast.

7–11. Spot localities in 'Murray's Gully', Tyers (see Fig. 1). We consider this body to be autochthonous, a repetition of the main Tyers–Boola development of Coopers Creek Limestone.

12. Limestone, including prominent stylobreccia, outcropping on the left bank of the Tyers River beneath the bridge about 750 m south-southwest of Tyers Quarry. The productive sample came from the left bank of the river a few metres downstream from the bridge abutment; samples from about the northern abutment of the bridge proved barren.

13. Oval nodules of mid-grey variably calcareous argillite mostly 6 cm or less but up to 20 cm in length, in rhythmically banded siltstones/argillites (?Wilson Creek Shale) outcropping in the bed of Seatabit Creek c. 15–20 m upstream from the crossing of the 'Gladstone Creek' 4-wheel drive road. Occasional fossils seen in cross-section are brachiopods, rugose corals and ?bactritids or Coleolus. No conodonts were found in the acid-insoluble residues.

14. A crinoidal limestone clast (not in situ) from Deep Creek c. 550 m upstream from its junction with Seatabit Creek, lithologically identical with the crinoidal limestone clast acid-leached from loc. 1.

15. White Rock (or Colonial Sugar Refineries) Quarry, Coopers Creek. Interpreted as allochthonous, emplaced within the Boola Formation. VandenBerg (1975) noted two megaclasts at this locality.

16. Evans Brothers Quarry, Coopers Creek. Cooper (1971) identified, inter alia, Eognathodus sulcatus from this locality. VandenBerg (1975) regards this megaclast as emplaced low within the Wilson Creek Shale.

17. Small outcrop of limestone on Platina–Coopers Creek road 460 m towards Coopers Creek from the bridge over the former Moe–Walhalla railway at Platina.

18. Megaclast of bioclastic limestone outcropping in a minuscule quarry on the Platina–Coopers Creek road 610 m towards Coopers Creek from the bridge over the former Moe–Walhalla railway at Platina.

19. Limestone spall, presumably from Evans

Fig 11. A–G, *Pandorinellina steinhornensis miae* (Bultynek 1971), all Pa elements. A, NMV P143089, lateral view, ×60, TQ/0-0.2. B, NMV P143090, lateral view, ×60, BOO16.5. C, NMV P143091, upper view, ×60, BOO16. D, NMV P143092, lower view, ×60, BOO13.8. E, NMV P143093, lateral view, ×60, BOO14.5. F, NMV P143094, lateral view, ×45, BOO43.8. G, NMV P143095, upper view, ×60, BOO20.1. H–L, *Ancyrodelloides omus* alpha morph Murphy & Matti 1983, all Pa elements. H, I, NMV P143096, upper and lower views respectively, ×60, BOO13.8. J, NMV P143097, upper view, ×45, BOO13.8. K, L, NMV P143098, upper and lower views respectively, ×45, BOO13.8.
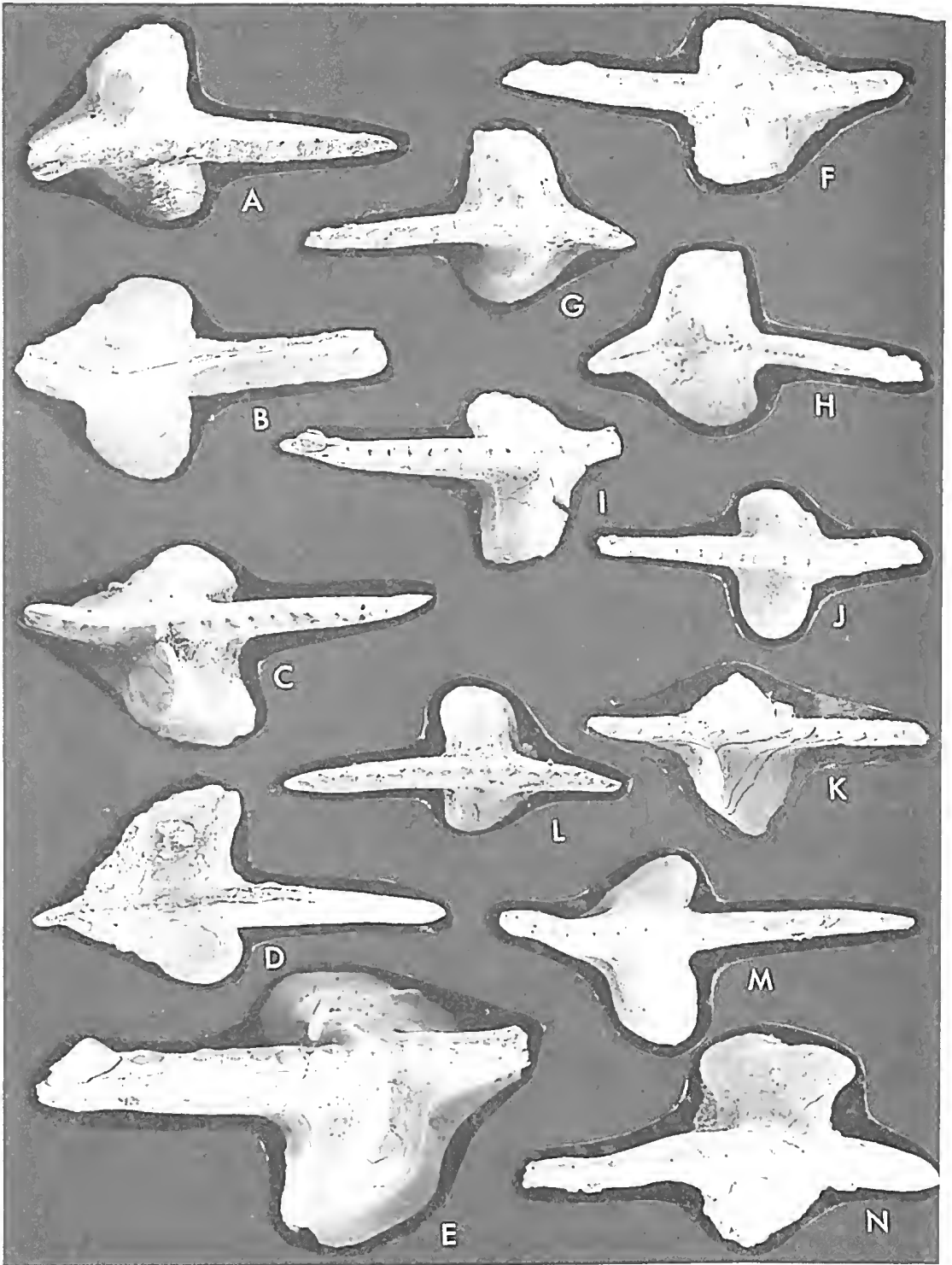
Brothers' Quarry, on old road upslope from Platina–Coopers Creek road, c. 350 m towards Coopers Creek from the bridge over the former Moe–Walhalla railway at Platina.

20. Loose blocks of conglomerate and conglomeratic sandstone with carbonate matrix in a gutter on the west side of Telbit Road (Thomas 1942) at grid reference 421961 on Vicmap 1:25 000 topographic map 8122-2-3 Tyers Junction. Samples from this locality, regarded as Boola Formation by VandenBerg (1975), were processed by Cooper (1971) and by us but no conodonts were obtained.

Nine limestone occurrences were not sampled:

21. An outcrop in the left branch of White's Creek, Tyers (Rehfisch & Webb 1993), interpreted as a northward extension of the Murray's Gully tract (locs 7–11).

22. An outcrop shown by Thomas (1942) between the White Rock and Evans Brothers quarries at Coopers Creek.

23. Limestone within the Wilson Creek Shale outcropping in the Thomson River about 0.65 km south-east of White Rock Quarry, Coopers Creek (Thomas 1942; Carey & Bolger ms.).

24. An occurrence of autochthonous limestone within the Wilson Creek Shale in Jacobs Creek, Moondarra (Carey & Bolger ms.)

25. An occurrence, now submerged beneath Lake Thomson, of 'highly fossiliferous limestone and calcareous strata partly metamorphosed by granodiorite' 'with a maximum width of about 20 feet and a length of 60–70 feet' outcropping on the east flank of the Thomson River '¼ mile south of Cascade Creek' (Baragwanath 1925, pp. 22 and 39, note 24).

26. Limestone clasts in conglomerate 'near the steel bridge (Poverty Point Bridge) over the Thomson River, about two miles north of its junction with Stringer's Creek' (Junner 1914, p. 289). A small sample from this locality has already failed to yield conodonts (Cooper 1971).

27. A body of limestone, assumed to be a clast, 'a couple of feet long and one foot thick, thinning out to nothing upwards and downwards and entirely enclosed by slates' reported by Murray (1895) as outcropping in the bed of Marble Creek.

28. A small occurrence reported by Kitson (1925, fig. 131) along strike northwards from the lower quarry at Marble Creek.

29. An outcrop reported by Herman (1901, p. 13) from Ostler's Creek, south of the Marble Creek limestone megaclasts and seemingly approximately on strike with them.

ACKNOWLEDGEMENTS

Fig. 12. A–N, *Ancyrodelloides omus* beta morph Murphy & Matti 1983, all Pa elements. A, B, NMV P143099, upper and lower views respectively, ×45, BOO7.8. C, D, NMV P143100, upper and lower views respectively, ×45, BOO6.2. E, NMV P143101, upper view, ×60, TQ loose. F, NMV P143102, upper view, ×60, TQ11.8–11.9. G, H, NMV P143103, upper and lower views respectively, ×45, BOO6.2. I, NMV P143104, upper view, ×60, BOO7.8. J, NMV P143105, upper view, ×45, BOO11.1. K, NMV P143106, upper view, ×45, TQ9.1. L, NMV P143107, upper view, ×45, TQ9.1. M, NMV P143108, upper view, ×45, TQ11.8–11.9. N, NMV P143109, upper view, ×60, TQ9.1.
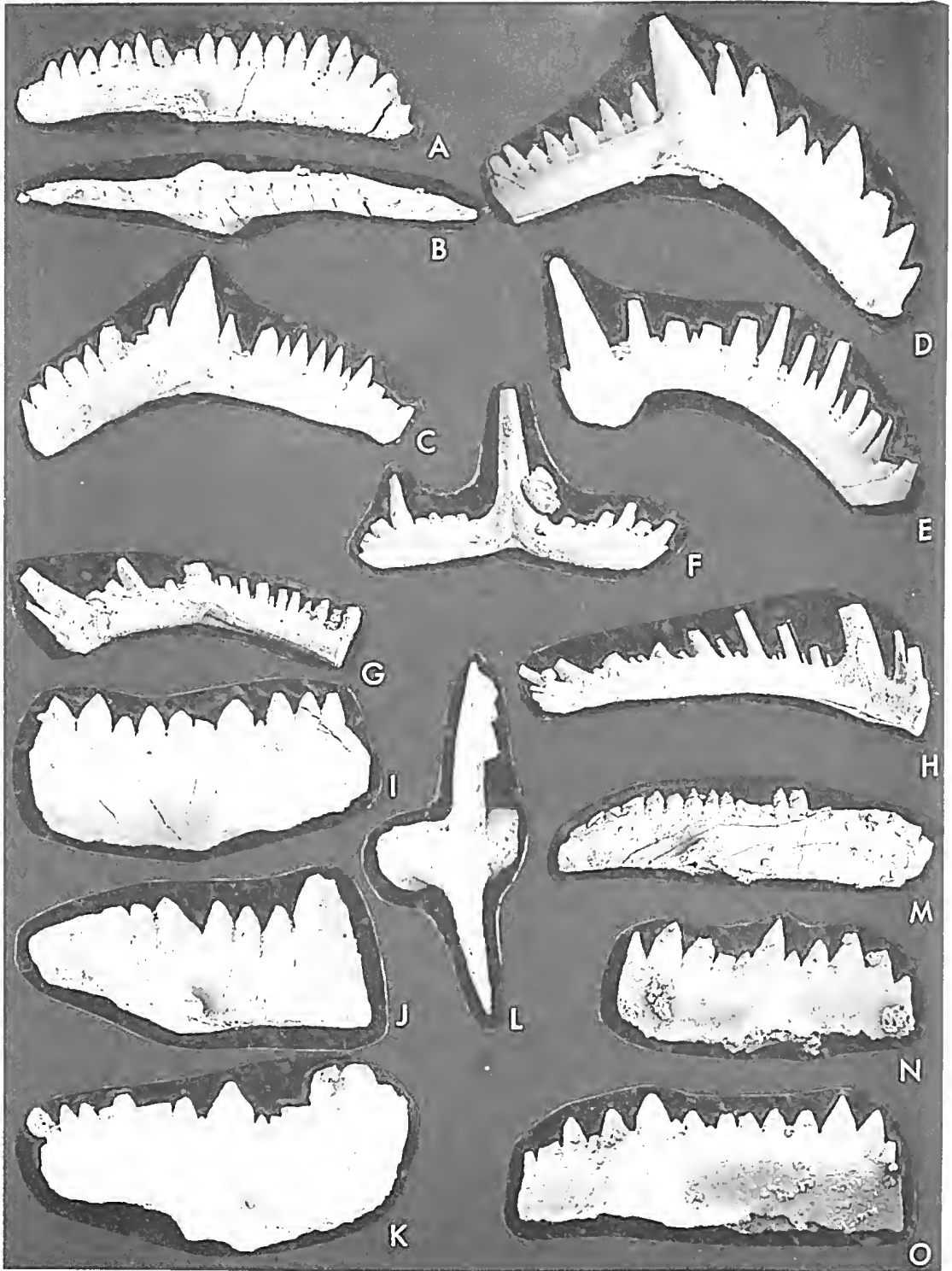
figures and Glenn Brock drew up the charts. Stephen Carey, John Pickett and Fons VandenBerg read and commented helpfully on the manuscript. We are grateful to all the above for their expertise, interest and support.

REFERENCES

AL-RAWI, D., 1977. Biostratigraphische Gliederung der Tentaculiten-Schichten des Frankenwaldes mit Conodonten und Tentaculiten (Unter- und Mittel-Devon; Bayern, Deutschland). *Senckenbergiana lethaea* 58: 25–79.

ARGENT, J. C., 1971. Stratigraphy and conodont biozonation of Lower Devonian limestones, Waratah Bay, Victoria, unpub. BA (Hons) thesis, Macquarie University, 169 p., 9 pls.

BARAGWANATH, W., 1925. The Aberfeldy district, Gippsland. *Memoirs of the Geological Survey of Victoria* 15, 45 p., 19 pls.

BISCHOFF, G. C. O. & ARGENT, J. C., 1990. Lower Devonian (Late Lochkovian–Pragian) limestone stratigraphy at [sic!] conodont distribution, Waratah Bay, Victoria. *Courier Forschungsinstitut Senckenberg* 118: 441–471.

BISCHOFF, G. C. O. & SANNEMANN, D., 1958. Unterdevonische Conodonten aus dem Frankenwald. *Notizblatt des hessischen Landesamtes für Bodenforschung* 86: 87–110.

BOERSMA, K. T., 1974. Description of certain Lower Devonian platform conodonts of the Spanish central Pyrenees. *Leidse geologische Mededelingen* 49: 285–301.

BOLGER, P. & CAREY, S., ms. Geology of the Deep Creek belt, Gippsland, Victoria.

BULTYNCK, P., 1971. Le Silurien supérieur et le Dévonien inférieur de la Sierra de Guadarrama (Espagne centrale). Deuxième partie: Assemblages de conodontes à *Spathognathodus*. *Bulletin de l'Institut royal des Sciences naturelles de Belgique* 46(3): 43 p., pls I–V.

BULTYNCK, P. & HOLLARD, H., 1980. Distribution comparée de conodontes et goniatites dévoniens des plaines du Dra, du Ma'der et du Tafilalt (Maroc). *Aardkundige Mededelingen* 1: 1–73.

CAREY, S. P. & BOLGER, P. F., ms. Conodonts of disparate ages from the Wilson Creek Shale (Lower Devonian, Victoria, Australia); stratigraphic implications.

CHAPMAN, F., 1903. New or little-known Victorian fossils in the National Museum, Victoria. Part II – Some Silurian Molluscoidea. *Proceedings of the Royal Society of Victoria* 16(1): 60–82, pls X–XII.

CHAPMAN, F., 1907. Newer Silurian limestones of eastern Victoria, Part I. *Records of the Geological Survey of Victoria* 2(1): 67–80, pls I–VIII.

CHAPMAN, F., 1912. Newer Silurian fossils of eastern Victoria, Part II. *Records of the Geological Survey of Victoria* 3(1): 224–233, pls XXXVIII–XXXVIII.

CHAPMAN, F., 1914. Newer Silurian fossils of eastern Victoria, Part III. *Records of the Geological Survey of Victoria* 3(3): 310–316, pls XLVI–LXI.

CHAPMAN, F., 1916. New or little-known Victorian fossils in the National Museum. Part 19, The Yeringian gastropod fauna. *Proceedings of the Royal Society of Victoria* 29: 75–103, pls II–VI.

CHAPMAN, F., 1921. New or little-known Victorian fossils in the National Museum. Part 25, Some Silurian tabulate corals. *Proceedings of the Royal Society of Victoria* 33: 212–225, pls IX–XI.

CHLUPAC, I., LUKES, P., PARIS, F. & SCHÖNLAUB, H. P., 1985. The Lochkovian–Pragian boundary in the Lower Devonian of the Barrandian. *Jahrbuch der geologischen Bundes-Anstalt in Wien* 128: 9–41.

CONAGHAN, P. J., MOUNTJOY, E. J., EDGECOMBE, D. R., TALENT, J. A. & OWEN, D. E., 1976. Nubrigyn algal reefs (Devonian), eastern Australia: allochthonous blocks and megabreccias. *Bulletin of the Geological Society of America* 87: 515–530.

COOPER, B. J., 1971 ms. Lower Devonian conodonts from the base of the Walhalla Group. *South Australian Department of Mines, Unpublished Report* DM757/75, 2 pp.

COOPER, B. J., 1973a. Lower Devonian conodonts from Loyola, Victoria. *Proceedings of the Royal Society of Victoria* 86: 77–84, pls 2, 3.

COOPER, B. J., 1973b. Discovery of Tentaculites in the limestone at Tyers, Gippsland. *The Victorian Naturalist* 90: 192–194.

DRUCE, E. C., 1970. Conodonts from the Garra Formation (Lower Devonian), New South Wales. *Australia, Bureau of Mineral Resources, Geology and Geophysics, Bulletin* 116: 29–64, pls 4–9.

FÅHRAEUS, L. E., 1971. Lower Devonian conodonts from the Michelle and Prongs Creek Formations, Yukon Territory. *Journal of Paleontology* 45: 665–683.

Fig. 13. A–H, *Ozarkodina excavata excavata* (Branson & Mehl 1933). A, Pa element, NMV P143110, lateral view, ×45, Loc. 4S. B, Pa element, NMV P143111, upper view, ×45, Loc. 4S. C, Pb element, NMV P143112, lateral view, ×45, Loc. 4S. D, Pb element, NMV P143113, lateral view, ×60, TQ6.6-6.7. E, M element, NMV P143114, lateral view, ×60, TQ6.6-6.7. F, Sa element, NMV P143115, lateral view, ×45, TQ7.3. G, Sb element, NMV P143116, lateral view, Loc. 4S. H. Sc element, NMV P143117, lateral view, ×45, Loc. 4S. I, *Ozarkodina remscheidensis repetitor* (Carls & Gandl 1969), Pa element, NMV P143118, lateral view, ×75, BOO6.2. J, *Ozarkodina ?confluens* (Branson & Mehl 1933), Pa element, NMV P143119, ×75, lateral view, Loc. 3A. K, L, *Pandorinellina optima* (Moskalenko 1966), Pa elements. K, NMV P143120, lateral view, ×90, BOO2.8. L, NMV P143121, upper view, ×45, Loc. 7. M, *Ozarkodina* sp., Pa element, NMV P, 143122, lateral view, ×30, TQ/0-0.2. N, O, *Ozarkodina remscheidensis remscheidensis* (Ziegler 1960), Pa elements, lateral views. N, NMV P143123, ×90, Loc. 3A. O, NMV P143124, ×60, Loc. 6.
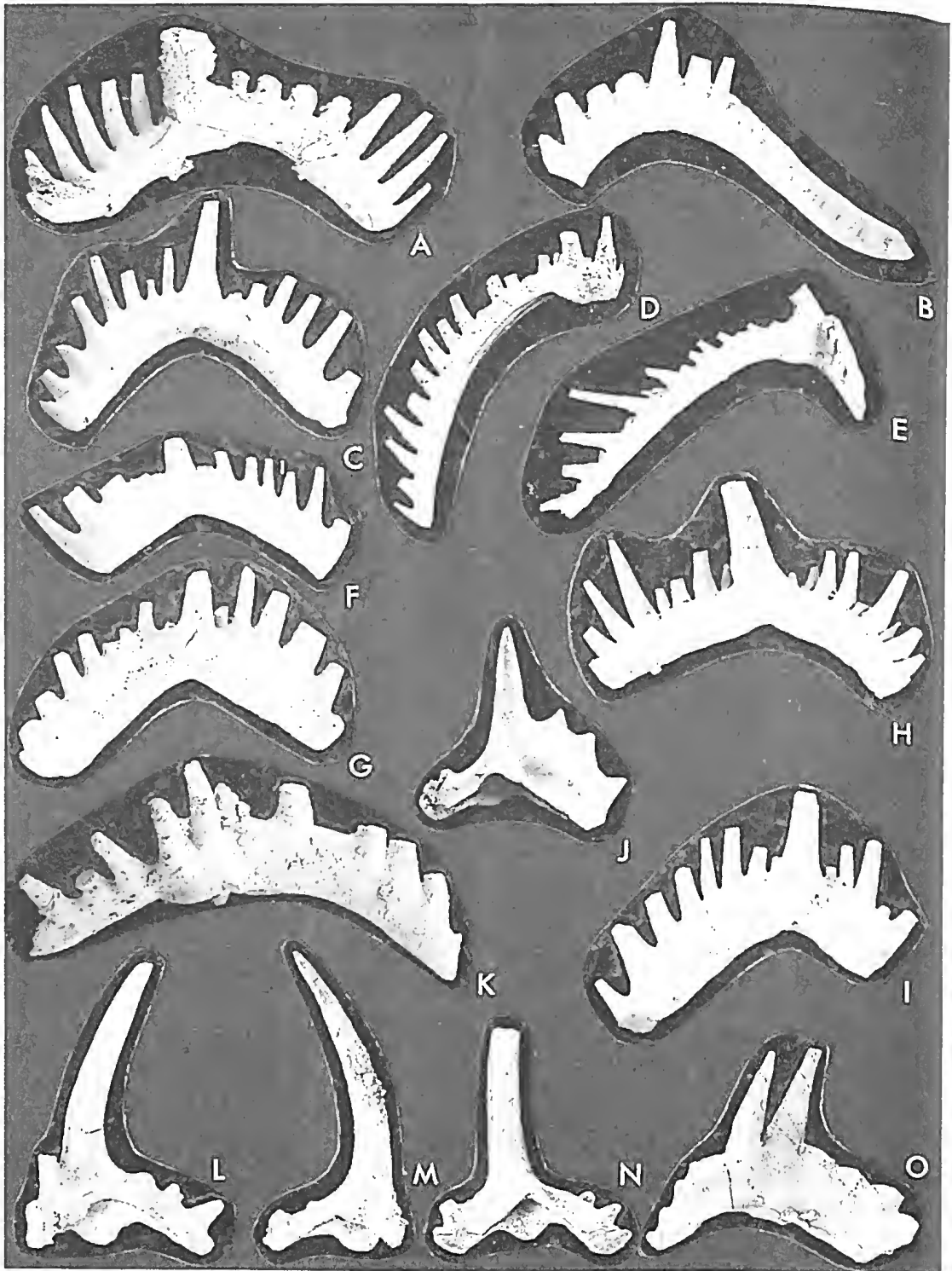
GARRATT, M. J., 1983a. Silurian to Early Devonian facies and biofacies patterns for the Melbourne Trough, central Victoria. *Journal of the Geological Society of Australia* 30: 121–147.

GARRATT, M. J., 1983b. Silurian and Devonian biostratigraphy of the Melbourne Trough, Victoria. *Proceedings of the Royal Society of Victoria* 95: 77–98.

GARRATT, M. J. & WRIGHT, A. J. T., 1989. Late Silurian to Early Devonian biostratigraphy of southeastern Australia. *Canadian Society of Petroleum Geologists* 14: 14(3): 647–667.

HERMAN, H., 1901. *Report on the Walhalla goldfield*. Special Report, Victorian Department of Mines, Melbourne, 65 p., 26 maps and sections.

HILL, D., 1978. Bibliography and index of Australian Palaeozoic corals. *Papers, Department of Geology, University of Queensland* 8(4): 38 p.

HOLLOWAY, D. J., 1991. *Azyptyx* gen. nov. (Trilobita, Cheirurinae) from the Lower Devonian of Victoria. *Alcheringa* 15: 235–242.

JAEGER, H., 1989. Devonian Graptoloidea. *Memoirs of the Canadian Society of Petroleum Geologists* 14(111): 431–438.

JELL, J. S. & HILL, D., 1969. Devonian corals from the Ukalunda district, north Queensland. *Publications of the Geological Survey of Queensland* 340: 1–27, pls 1–9.

JUNNER, N. R., 1915. On the occurrence of igneous pebbles in a conglomerate of Upper Silurian age from near Walhalla. *Proceedings of the Royal Society of Victoria* 27(N.S.): 286–296, pl. 11.

JUNNER, N. R., 1920. The geology and ore deposits of the Walhalla–Woods Point auriferous belt. *Proceedings of the Australian Institute of Mining and Metallurgy* 39: 127–258.

KENNY, J. P. L., 1937. Tyers River limestone. *Records of the Geological Survey of Victoria* 5(4): 702–704, pl. 21.

KITSON, A. E., 1925. Silurian limestone at Marble Creek, Thomson River. *Records of the Geological Survey of Victoria* 4(4): 443–446.

KLAPPER, G., 1969. Lower Devonian conodont sequence, Royal Creek, Yukon Territory, and Devon Island, Canada; with a section on Devon Island stratigraphy by A. R. Ormiston. *Journal of Paleontology* 43: 1–27.

KLAPPER, G., 1977. Lower and Middle Devonian conodont sequence in central Nevada; with contributions by D. B. Johnson. *University of California Riverside, Campus Museum Contributions* 4: 33–54.

KLAPPER, G. & JOHNSON, D. B., 1975. Sequence in the conodont genus *Polygnathus* in Lower Devonian at Lone Mountain, Nevada. *Geologica et Palaeontologica* 9: 65–77, pls 1–3.

KLAPPER, G. & JOHNSON, J. G., 1980. Endemism and dispersal of Devonian conodonts. *Journal of Paleontology* 54: 400–455.

KLAPPER, G. & MURPHY, M. A., 1980. Conodont zonal species from the *delta* and *pesavis* Zones (Lower Devonian) in central Nevada. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1980(8): 490–504.

KLAPPER, G. & PHILIP, G. M., 1971. Devonian conodont apparatuses and their vicarious skeletal elements. *Lethaia* 4: 429–452.

KLAPPER, G. & PHILIP, G. M., 1972. Familial classification of reconstructed Devonian conodont apparatuses. *Geologica et Palaeontologica* SB1: 197–113.

KNIGHT, J. B., COX, L. R., KEEN, A. M., BATTEN, R. L., YOCHELSON, E. L. & ROBERTSON, R., 1960. Systematic descriptions. *Treatise on Invertebrate Paleontology, Part 1, Mollusca 1*. Geological Society of America, Inc., and University of Kansas, New York, and Lawrence, Kansas, 1169–1331.

LANE, H. R. & ORMISTON, A. E., 1979. Siluro–Devonian biostratigraphy of the Salmontrout River area, east-central Alaska. *Geologica et Palaeontologica* 13: 39–96, 12 pls.

LENZ, A. C., 1989. Revision of Upper Silurian and Lower Devonian graptolite biostratigraphy and morphological variation in *Monograptus yukonensis* and related Devonian graptolites, northern Yukon, Canada. *Memoirs of the Canadian Society of Petroleum Geologists* 14(111): 439–447.

MASHKOVA, T. V., 1978. Drevneyshie konodontovye kompleksy devona SSSR. *Sovetskaya Geologiya* 1978(4): 3–14.

MAWSON, R., 1986. Early Devonian (Lochkovian) conodont faunas from Windellama, New South Wales. *Geologica et Palaeontologica* 20: 39–71.

MAWSON, R., 1987a. Early Devonian conodont faunas from Buchan and Bindi, Victoria, Australia. *Palaeontology* 30: 251–297, pls 31–41.

MAWSON, R., 1987b. Documentation of conodont assemblages across the Early Devonian–Middle Devonian boundary, Broken River Formation, North Queensland, Australia. *Courier Forschungsinstitut Senckenberg* 92: 251–273.

MAWSON, R., 1993. *Bipennatus*, a new genus of Devonian conodonts. *Memoirs of the Australasian*

Fig. 14.   A–1, *Oulodus* cf. *walliseri* (Ziegler 1960), all lateral views. A, Pa element, NMV P143125, ×45, Loc. 3C. B, Pb element, NMV P143126, ×45, TQ11.8–11.9. C, G, 1, Sa elements. C, NMV P143127, ×45, TQ11.8–11.9. G, NMV P143131, ×45, BOO11.1.1, NMV P143133, ×45, BOO1.8. D, M element, NMV P143128, ×45, Loc. 4W. E, Sc element, NMV P143129, ×45, Loc. 4W. F, H, Sb elements. F, NMV P143130, ×45, BOO1. H, NMV P143132, ×45, Loc. 9. J, *?Amydrotaxis* Pb element, NMV P143134, ×45, BOO72. K, *?Erika* sp. Pa element, NMV P143135, ×60, Loc. 4W. L–N, *Oulodus* sp. L, Sb element, NMV P143136, ×45, BOO43.7. M, Sc element, NMV P143137, ×45, BOO23. N, Sa element, NMV P143138, ×45, BOO45. O, Pathological form of *Oulodus* Pb element, NMV P143139, ×60, BOO70.
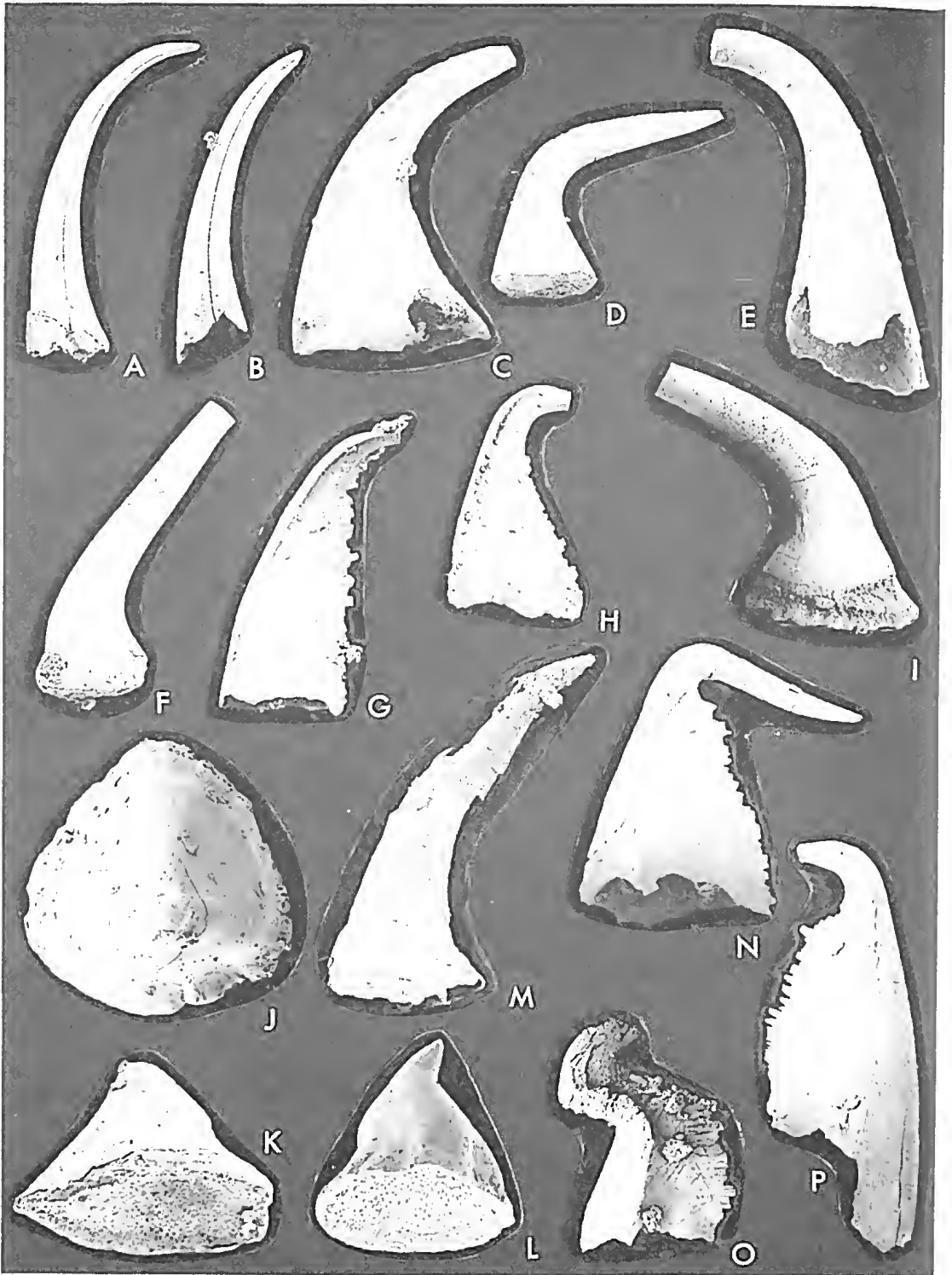
Association of Palaeontologists 15: 137–140.

MAWSON, R. & TALENT, J. A., 1989. Late Emsian–Givetian stratigraphy and conodont biofacies – carbonate slope and offshore shoal to sheltered lagoon and nearshore carbonate ramp – Broken River, North Queensland, Australia. *Courier Forschungsinstitut Senckenberg* 117: 205–259.

MAWSON, R., TALENT, J. A., BEAR, V. C., BENSON, D. S., BROCK, G. A., FARRELL, J. R., HYLAND, K. A., PYEMONT, B. D., SLOAN, T. R., SOREN-TINO, L., STEWART, M. I., TROTTER, J.A., WILSON, G. A. & SIMPSON, A. G., 1988. Conodont data in relation to resolution of stage and zonal boundaries for the Devonian of Australia. *Memoir of the Canadian Society of Petroleum Geologists* 14: 485–527.

MAWSON, R., TALENT, J. A., BROCK, G. A. & ENGEL-BRETSEN, M. J., 1992. Conodont data in relation to sequences about the Pragian–Emsian boundary (Early Devonian) in southeastern Australia. *Proceedings of the Royal Society of Victoria* 104: 23–56.

MURPHY, M. A., 1989. Lower Pragian boundary (Lower Devonian) and its application in Nevada. *Courier Forschungsinstitut Senckenberg* 117: 61–70.

MURPHY, M. A. & MATTI, J. C., 1983. Lower Devonian conodonts (*hesperius-kindlei* zones), central Nevada. *University of California Publications of Geological Science* 123: 1–82.

MURPHY, M. A., MATTI, J. C. & WALLISER, O. H., 1981. Biostratigraphy and evolution of the *Ozarkodina remscheidensis-Eognathodus sulcatus* lineage (Lower Devonian) in Germany and central Nevada. *Journal of Paleontology* 55: 747–772, 3 pls.

MURRAY, R. A. F., 1876. Report on the geology and mineral resources of south-western Gippsland. *Progress Report of the Geological Survey of Victoria* 3: 142–143.

MURRAY, R. A. F., 1878. Geological sketch map, sheet 2, south-east Gippsland. *Progress Report of the Geological Survey of Victoria* 5: 44–70.

MURRAY, R. A. F., 1887. *Victoria: geology and physical geography.* Government Printer, Melbourne, 179 p.

MURRAY, R. A. F., 1889. The limestone on the Tyers River. The Goldfields of Victoria. Reports of the Mining Registrars for the quarter ending 30th September, 1889, p. 68–69.

MURRAY, R. A. F., 1895. *Victoria: geology and physical geography,* second edition. Government Printer, Melbourne, 150 p.

PEDDER, A. E. H., 1965. A revision of the Australian Devonian corals previously referred to *Micto-phyllum*. *Proceedings of the Royal Society of Victoria* 78: 201–220, pls 30–34.

PEDDER, A. E. H., 1967. *Lyrielasma* and a new related genus of Devonian tetracorals. *Proceedings of the Royal Society of Victoria* 80: 1–30, pls 1–7.

PHILIP, G. M., 1960a. The Middle Palaeozoic squamulate favositids of Victoria. *Palaeontology* 3: 186–207, pls 30–34.

PHILIP, G. M., 1960b. Victorian Siluro-Devonian faunas and correlations. *International Geological Congress, Report of Twenty-first Session, Norden* 7: 143–157.

PHILIP, G. M., 1961. Lower Devonian crinoids from Toongabbie, Victoria, Australia. *Geological Magazine* 98: 143–160, pl. 8.

PHILIP, G. M., 1962. The palaeontology and stratigraphy of the Siluro-Devonian sediments of the Tyers area, Gippsland, Victoria. *Proceedings of the Royal Society of Victoria* 75: 123–246, pls XI-XXXVI.

PHILIP, G. M., 1965. Lower Devonian conodonts from the Tyers area, Gippsland, Victoria. *Proceedings of the Royal Society of Victoria* 79: 95–117, pls 8–10.

PHILIP, G. M., 1968. Late Silurian-Early Devonian relationships in the central Victorian and western Tasmanian clastic sequences, Australia. In *International Symposium on the Devonian System, Calgary 1967*, Oswald, D. H., ed., Alberta Society of Petroleum Geologists, Calgary, vol. 2, p. 913–920.

PICKETT, J. W., 1980. Conodont assemblages from the Cobar Supergroup (Early Devonian), New South Wales. *Alcheringa* 4: 67–88.

REHFISCH, M. W. & WEBB, J. A., 1993. The Early Devonian Coopers Creek Limestone, a redeposited deep-water limestone within the Melbourne Trough, southeastern Australia. *Australian Journal of Earth Science* 40: 575–589.

SAVAGE, N. M., 1973. Lower Devonian biostratigraphic correlation in eastern Australia and western North America. *Lethaia* 5: 341–348.

SAVAGE, N. M., 1977. Lower Devonian conodonts from the Karheen Formation, southeastern Alaska. *Canadian Journal of Earth Sciences* 14: 278–284.

SAVAGE, N. M., CHURKIN, M., JR, & EBERLEIN, G. D., 1977. Lower Devonian conodonts from Port St Nicholas, southeastern Alaska. *Canadian Journal of Earth Sciences* 14: 2928–2936.

Fig. 15. All except J are lateral views. A, *Neopanderodus aequabilis* Telford 1975, NMV P143140, ×45, BOO/0. B, *Panderodus unicostatus* (Branson & Mehl 1933), NMV P143141, ×45, BOO6.2. C, E, *Panderodus valgus* (Philip 1965). C, NMV P143142, ×90, TQ6.6–6.7. E, NMV P143144, ×90, TQ6. D, *Panderodus recurvatus* (Rhodes 1953), NMV P143143, ×75, BOO13.8. F, I, M, *Drepanodus* sp. F, NMV P143145, ×60, BOO13.8. I, NMV P143148, ×60, BOO23. M, specimen showing breakage, NMV P143152, ×75, Loc. 17. G, H, *Belodella resima* (Philip 1965). G, NMV P143146, ×75, BOO/0. H, NMV P143147, ×75, BOO/0. J-L, *Pseudooneotodus beckmanni* (Bischoff & Sannemann 1958). J, NMV P143149, upper view, ×90, TQ6.6–6.7. H, NMV P143150, ×90, TQ6.6–6.7. L, NMV P143151, ×90, TQ6.6–6.7. N-P, *Belodella triangularis* (Stauffer 1940). N, NMV P143153, ×90, BOO3.8. O, Pathological specimen, NMV P143154, ×60, BOO/0. P, NMV P143155, ×60, BOO49.
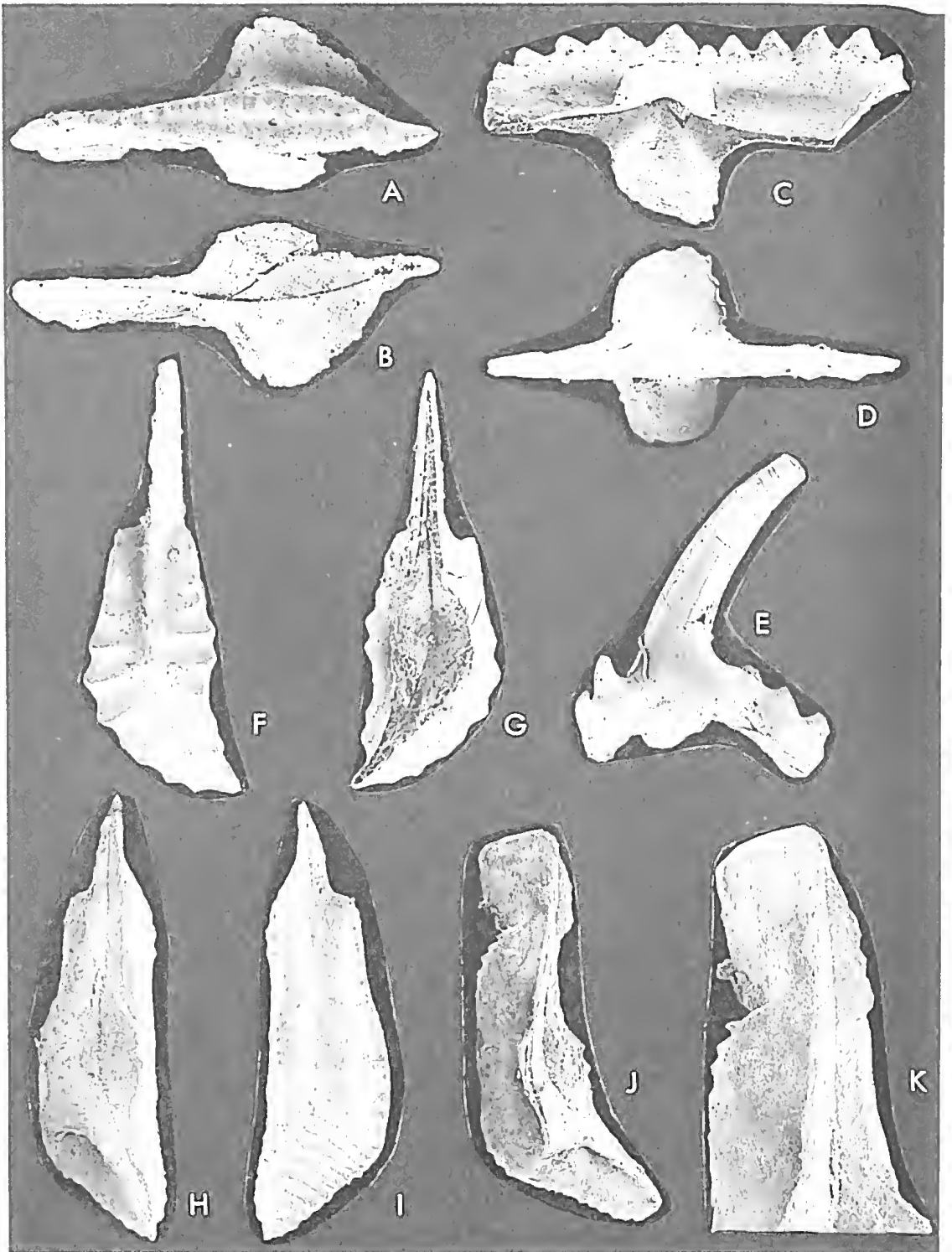
SAVAGE, N. M. & GEHRELS, G. E., 1984. Early Devonian conodonts from Prince of Wales Island, south-eastern Alaska. *Canadian Journal of Earth Sciences* 21: 1415–1425.

SCHÖNLAUB, H. P., 1985. Devonian conodonts from section Oberbuchach II in the Carnic Alps (Austria). *Courier Forschungsinstitut Senckenberg* 75: 353–374, 6 pls.

SKEATS, E. W., 1928. Stratigraphical and structural relations of Silurian rocks of Walhalla–Wood's Point district, Victoria, in relation to the 'Tanjilian' Series. *Australasian Association for the Advancement of Science* 19: 219–230.

STRUSZ, D. L., 1966. Spongophyllidae from the Devonian Garra Formation, New South Wales. *Palaeontology* 9: 544–598, pls 85–96.

STRUSZ, D. L., 1968. On *Cyathophyllum mansfieldense* Dun 1898: Lower Devonian, Loyola, Victoria. *Proceedings of the Royal Society of Victoria* 81: 11–18, pl. 2.

SWEET, W. C., 1988. *The Conodonta: morphology, taxonomy, paleoecology and evolutionary history of a long-extinct animal phylum* (Oxford Monographs on Geology and Geophysics No. 10), Clarendon Press, Oxford, 212 p.

TALENT, J. A., 1956a. Devonian brachiopods and pelecypods of the Buchan Caves Limestone, Victoria. *Proceedings of the Royal Society of Victoria* 68: 1–56, pls I–V.

TALENT, J. A., 1956b. Siluro-Devonian brachiopods from Marble Creek, Thomson River, Victoria. *Proceedings of the Royal Society of Victoria* 68: 73–84, pls VIII–X.

TALENT, J. A., 1965. The stratigraphic and diastrophic evolution of central and eastern Victoria in Middle Palaeozoic times. *Proceedings of the Royal Society of Victoria* 79: 179–195.

TALENT, J. A., 1989. Transgression-regression pattern for the Silurian and Devonian of Australia. In *Pathways in geology—essays in honour of Edwin Sherbon Hills*, Le Maitre, R. W., ed., 201–219. Distributed by Blackwells, Carlton.

TALENT, J. A., GRATSIANOVA, R. T. & YOLKIN, E. A., 1995. Latest Silurian (Pridoli) to Middle Devonian (Givetian) of the Asia–Australia hemisphere: rationalization of brachiopod taxa and faunal lists; stratigraphic correlation chart. *Courier Forschungsinstitut Senckenberg* (in press).

TALENT, J. A. & PHILIP, G. M., 1956. Siluro-Devonian Mollusca from Marble Creek, Thomson River, Victoria. *Proceedings of the Royal Society of Victoria* 68: 57–71, pls VI, VII.

TASSELL, C. B., 1977. Gastropods from some Early Devonian limestones of the Walhalla Synclinorium. *Memoirs of the National Museum of Victoria* 38: 231–245, pl. 7.

TASSELL, C. B., 1982. Some Siluro-Devonian rostroconch molluscs from south-eastern Australia. *Records of the Queen Victoria Museum* 79: 1–11.

TEICHERT, C., 1954. Note on Devonian limestones between The Bluff and Bird Rock, Waratah Bay, Victoria. *Proceedings of the Royal Society of Victoria* 66: 103–104.

TELFORD, P. G., 1975. Lower and Middle Devonian conodonts from the Broken River Embayment, North Queensland, Australia. *Special Papers in Palaeontology* 15: 96 pp.

THOMAS, D. E., 1942. The conglomerates in the Gould–Platina districts, Gippsland, Victoria. *Mining and Geological Journal (Victoria)* 2(6): 357–360.

UYENO, T. T., 1990. Biostratigraphy and conodont faunas of Upper Ordovician through Middle Devonian rocks, eastern Arctic Archipelago. *Bulletin of the Geological Survey of Canada* 401: 211 p.

UYENO, T. T., 1991. Pre-Famennian Devonian conodont biostratigraphy of selected intervals in the eastern Canadian Cordillera. *Bulletin of the Geological Survey of Canada* 417: 129–161.

VANDENBERG, A. H. M., 1975. Definitions and description of Middle Ordovician to Middle Devonian rock units of the Warburton district, east central Victoria. *Geological Survey of Victoria, Report* 1975/6, 65 p.

VANDENBERG, A. H. M., 1977a. Explanatory notes on the Warburton 1:250 000 geological map. *Geological Survey of Victoria, Report* 47 (1977/7), 54 p.

VANDENBERG, A. H. M. (compiler), 1977b. *Warburton 1:250 000 geological map, sheet SJ55-6*. Geological Survey of Victoria, Melbourne.

VANDENBERG, A. H. M., 1988. Silurian-Middle Devonian. In *Geology of Victoria*, 2nd edn, J. G. Douglas & J. A. Ferguson, eds, Victorian division of the Geological Society of Australia, 103–146.

VANDENBERG, A. H. M. & GARRATT, M. J., 1976. Melbourne Trough. *Geological Society of Australia Special Publication* 5: 45–62.

VANDENBERG, A. H. M. & SCHLEIGER, N. W., 1972. Palaeogeography and tectonic significance of diachronism in Siluro-Devonian age flysch sediments, Melbourne Trough, south-eastern Australia: discussion. *Bulletin of the Geological Society of America* 83: 1565–1570.

Fig. 16. A, B, *Eognathodus sulcatus* Philip 1965, lambda morph. NMV P143156, upper and lower view respectively, ×60, Loc. 16. C, D, *Ozarkodina pseudomiae* Mawson 1992. NMV P143157, lateral and upper views respectively, ×90, Loc. 12. E, *Oulodus* sp. NMV P143158, ×45. F–K, *Polygnathus dehiscens* Philip & Jackson 1967. F, G, Juvenile specimen, NMV P143159, upper and lower views respectively, ×75, Loc. 12. H–K, New SEM photographs of holotype, University of New England F9173/1, lower, upper and two lateral views respectively. H–J, ×55. K, ×100, from the Cavan Formation 'in road cutting *c.* 350 yards W. of Taemas Bridge, Taemas, southern N.S.W.' (Philip & Jackson 1967). Note the damaged basal cavity in H, J and K.

WANG, C.-Y., RUAN, Y.-P., MU, D.-C., WANG, Z.-H., RONG, J.-Y., YIN, B.-A., KUANG, G.-D., & SU, Y-B., 1979. Subdivision and correlation with Europe. *Acta Stratigraphica Sinica* 3: 305–311.

WEBB, J. A., 1991. Geological history of Victoria. In Cochrane, G. W., *et al.* (eds), *Introducing Victorian Geology*. Geological Society of Australia, Victorian Division, Melbourne, p. 67–168.

WEBBY, B. D., STEARN, C. W. & ZHEN, Y. Y., 1993. Lower Devonian (Pragian–Emsian) stromatoporoids from Victoria. *Proceedings of the Royal Society of Victoria* 105: 113–185.

WEDDIGE, K., 1987. The lower Pragian boundary (Lower Devonian) based on the conodont species *Eognathodus sulcatus*. *Senckenbergiana lethaea* 67: 479–497.

WEDDIGE, K., 1990. Pathological conodonts. *Courier Forschungsinstitut Senckenberg* 118: 563–589.

WEIR, J. C., FENTON, M. W., TOMLINSON, K. M. & WILSON, C. J. L., 1988. Sedimentology of the Early Devonian Walhalla Group at Walhalla, Victoria. *Australian Journal of Earth Sciences* 35: 405–419.

WHITELAW, O. A. L., 1916. The topography, geology and mines of the Woods Point district. *Memoirs of the Geological Survey of Victoria* 13: 32 p., 33 pls.

WILSON, G. A., 1989. Documentation of conodont assemblages across the Lochkovian–Pragian (Early Devonian) boundary at Wellington, central New South Wales, Australia. *Courier Forschungsinstitut Senckenberg* 117: 117–171.

WINCHESTER-SEETO, T., 1993. Documentation of chitinozoan assemblages from the Pragian (Early Devonian) of eastern Australia. *Proceedings of the Royal Society of Victoria* 105: 85–112.

YOLKIN, E. A., APEKINA, L. S., ERINA, M. V., IZOKH, N. G., KIM, A. I., TALENT, J. A., WALLISER, O. H., WEDDIGE, K. W., WERNER, R. & ZIEGLER, W., 1989. Polygnathid lineages across the Pragian–Emsian boundary, Zinzilban Gorge, Zerafshan, USSR. *Courier Forschungsinstitut Senckenberg* 110: 237–246.

ZIEGLER, W. (ed.), 1973. Catalogue of conodonts, 1, E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 504 pp., 27 pls.

ZIEGLER, W. (ed.), 1975. *Ibid*. II, 404 pp., 25 pls.

ZIEGLER, W. (ed.), 1977. *Ibid*. III, 574 pp., 39 pls.

ZIEGLER, W. (ed.), 1981. *Ibid*. IV, 445 pp., 41 pls.

ZIEGLER, W. (ed.), 1991. *Ibid*. V, 212 pp., 13 pls.

PALEOCENE BIVALVES FROM THE PEBBLE POINT FORMATION, VICTORIA, AUSTRALIA

THOMAS A. DARRAGH

Museum of Victoria, 285 Russell Street, Melbourne, Victoria 3000

Thirty-two bivalve taxa are recorded from the Paleocene Pebble Point Formation, Otway Basin, Victoria, Australia, of which 11 are newly described and 17 are recorded in open nomenclature. New species are *Lamellinucula pyrenoides, Australoneilo cultrata, Limopsis rupestris, Myrtea faseolata, Cyamiocardium silicula, Astarte (Astarte) notialis, Venericardia (Rotundicardia) petraea, Carditellopsis bellissima, Bertinella lapidaria, Dosinia (Dosinobia) saxatilis, Callistina (Tikia)? scopulensis.* The environment was one of high energy, shallow water and the climate was probably cool temperate. The fauna is composed mostly of genera that were cosmopolitan during the Paleocene and shows no close affinity with any other, suggesting considerable isolation from other Paleocene faunas. *Lahillia* and *Australoneilo* are the only taxa with a particular Antarctic and South American affinity and *Lahillia, Dosinia (Dosinobia)* and *Callistina (Tikia)?* have an affinity with New Zealand. *Eotrigonia* is the only endemic genus present.

Keywords: Bivalvia, Late Paleocene, Otway Basin, Victoria, Australia, palaeoecology, biogeography, taxonomy, new taxa.

PALEOCENE MOLLUSCAN FAUNAS occur in Australia in the Carnarvon, Perth and Otway Basins, but despite their importance have received little attention. Factors in this neglect are the restricted and poor outcrop, the sparsely fossiliferous nature of the rocks and the very hard matrix making extraction difficult.

Paleocene faunas are potentially important in providing clues to the origin of the later Tertiary faunas of Australia and to the nature of the fauna present in the region at the time of the separation of the Australian plate from the Antarctic plate. They are also critical for understanding the faunal recovery and evolutionary radiation following the end-Cretaceous mass extinction.

The bivalves described here occur in the Pebble Point Formation in the Otway Basin, Western Victoria. Of the other Paleocene formations of Australia, the Cardabia Calcarenite (including the Boongarooda Greensand Member, Wadera and Pirie Members) in the Carnarvon Basin, Western Australia contains few bivalves and there is nothing in common with the Pebble Point Formation; the King's Park Shale in the Perth Basin is known only from subsurface (McGowran 1964).

Molluscs now known to be of Paleocene age were first collected by C. S. Wilkinson from Pebble Point (his locality Aw 6) during his geological survey of the Otway Ranges and coast in 1864 (Wilkinson 1865). The molluscs were never described, though McCoy (1876) recorded *Cucullaea* *corioensis* 'very thick variety' from east of the Gellibrand River based on Wilkinson's collection.

PREVIOUS WORK

The only formally named molluscs in the fauna of the Pebble Point Formation are two nautiloid cephalopods, *Aturoidea distans* and *Nautilus victorianus* (Teichert 1943); three bivalves, *Nuculana paucigradata, Cucullaea (Cucullona) psephea* and *Lahillia australica*, and a scaphopod, *Dentalium (Fissidentalium) gracilicostatum* (Singleton 1943), all described from collections made by George Baker, who studied the stratigraphy and sediments of the coastline between Moonlight Head and Curdies Inlet (Baker 1943). Teichert (1943) and Singleton (1943) recognised that the fauna was the oldest known from the Australian Tertiary. Teichert concluded that the age was Eocene and Singleton that the age was Early Eocene or possibly Paleocene. Singleton recognised links between the bivalves and those in South America, Antarctica and New Zealand.

In 1986 Darragh described a further bivalve, *Eotrigonia paleocenica.*

The foraminiferal fauna was described by McGowran (1965), who concluded that it was of middle Paleocene age, correlated with Zone P3, *Globorotalia pusilla pusilla–Globorotalia angulata* zone. Later McGowran (1991) refined this cor-

relation, stating that the Pebble Point marine transgression fell near the P4/P5 boundary, late Paleocene (Thanetian or Seelandian).

LOCALITY AND NATURE OF FORMATION

The Pebble Point Formation outcrops in coastal cliffs between Moonlight Head and the mouth of the Gellibrand River. It transgressively overlaps the early Cretaceous Otway Group sediments and is conformably overlain by the Dilwyn Formation (Late Paleocene–Early Eocene) (Baker 1950). Molluscs are extremely rare in the formation. Inland it outcrops in western Victoria in the valleys of the Wannon River and Grange Burn west of Hamilton and at Killara Bluff on the Glenelg River and opposite at Bahgallah south of Casterton. These inland outcrops are highly ferruginised and weathered. No carbonate has survived and fossils are difficult to determine. At Killara Bluff where the calcium carbonate of the fossils has been replaced by limonite (Kenley 1951, 1971), Kenley (1954) recorded 16 m of ferruginous sands and fine conglomerates containing *Nuculana paucigradata, Cucullaea (Cucullona) psephea, Eotrigonia* sp., *Lahillia australica, Panopea* sp. and *Aturoidea distans.*

Spencer-Jones (1971) recorded thick-bedded, heavily ferruginised coarse to fine gravels, coarse and fine sandstone, pebbly sandstone and limonitic siltstone in the valleys of the Wannon River and Grange Burn in the area of the Parkhill and Morgiana Estates and extending southwest to the Miakite Creek valley. A maximum thickness of 61 metres was recorded near the Parkhill Estate southwest of Wannon. These sediments overlap the Late Cretaceous Otway Group sediments and in turn are overlain by formations of the Oligocene to Miocene Heytesbury Group.

Fossils, abundant at some localities, are found in these sediments as moulds, but in most cases so ferruginised that determination is not possible. At some localities where the ferruginous siltstones outcrop, well preserved moulds can be found which enable a determination to be made. Fossils collected by D. Spencer-Jones in 1964 from two such localities have been examined. The bivalve fauna is reasonably diverse and all determinable fossils occur in the Pebble Point Formation on the coast. Therefore, it is reasonable to infer that these ferruginous sediments are a lateral extension of the Pebble Point Formation. This means that the Paleocene marine incursion in the Otway Basin was far more extensive than previously realised and extends inland nearly as far as the later Miocene incursion.

On the Otway coast the formation consists of 20–30 m of coarse quartzose sandstone, grits, conglomerate and gritty ferruginous clays (Baker 1950). When fresh the rock matrix has a bluish colour. In outcrop along the coast it is highly ferruginous and cemented owing to oxidation, but the carbonate fossils are still preserved. Fossils are not uniformly distributed but found in a narrow band about 3 m thick about 10 m above the base of the formation. Other macrofossils present are rare solitary corals, shark teeth, fish vertebrae and crab remains.

Matrix adhering to the fossils is very fine-grained, limonitic, often cemented, with fine to coarse quartz grains embedded in it. In less weathered matrix glauconite pellets are common. The ferruginous matrix contains siderite which in many cases bonds chemically to the shell smothering fine detail of the shell surface. It is impossible to remove this coating without damage to the shell itself.

Since it is very difficult to collect fossils *in situ*, recourse has to be made to beach boulders, from which most fossils have been collected. Fossils in partially weathered boulders can be separated from the matrix by careful picking with needles. Fossils exposed on the surface of indurated boulders can only be collected with hammer and chisel and their preparation is extremely difficult and time-consuming.

Locality

The details of the localities from which material was collected are as follows. The numbers are from the Museum of Victoria fossil locality register and are used throughout to save repetition.

PL 3001   SE side of Dilwyn Cove, N side of Bell Point, 6 km SE of Princetown, from boulders on beach derived from 0.5 m grey (weathered) sandstone about 15 m above beach, Victoria, Princetown 903100.

PL 3002   N side of Dilwyn Cove, S side of Pebble Point, G.S.V. loc. Aw6, 5 km SE of Princetown, Victoria, Princetown 900103.

PL 3003   Cove between Buckley Point and Point Pember, 4.5 km SE of Princetown, Victoria, Princetown 894109.

PL 3004   Shelly band about 10 m above beach, NW side of Buckley Point, 4 km SE of Princetown, Victoria, Princetown 894109.

PL 3005   W end of large slip at Killara Bluff at top section, allot. 4, sect. A, Parish of Killara, Victoria, Dartmoor WD313291.

PL 3006   Ironstone about 100 m above river, right

bank of Glenelg River on Hazell Bank, Bahgallah, Victoria, Dartmoor WD324296.

PL3176 Cutting on Morgiana Road, about 5 km south of Wannon, left bank Grange Burn, Coleraine WD 760267.

PL3177 South flowing gully running into right bank of Grange Burn, about 0.5 km south of Clayton's Road, 3.5 km southeast of Wannon, Coleraine WD729253.

Most of the material described here was collected from fallen boulders at PL3003.

ENVIRONMENT AND DEPOSITION

Baker (1950) suggested that the Pebble Point Formation consisted of littoral, shallow-water deposits and McGowran (1965) stated that the foraminifera indicated a shallow-water, open marine environment. The bivalves suggest a similar environment. A majority of specimens show signs of abrasion suggesting that the specimens were transported some distance before burial. There are few articulated pairs of valves extant. Of these pairs, specimens of *Bertinella? lapidaria* sp. nov. are the most common. Even the infaunal species, such as *Panopea* sp., have the valves disarticulated suggesting exhumation after death. Many species have heavy robust shells. Such evidence, together with the coarse particles in the host rock, suggest a high energy, shallow-water environment.

BIVALVE FAUNA

There are 32 taxa recorded here but three are represented by such poor material that comparison with other taxa is not possible. In addition there are two other taxa whose relationships are not clear as the material available may consist of juveniles. The fauna so far identified is as follows:

Nuculidae	*Lamellinucula pyrenoides* sp. nov.
Nuculanidae	*Comitileda* sp.
	Ledina paucigradata Singleton
	Neilo (Australoneilo) cultrata sp. nov.
Cucullaeidae	*Cucullaea psephea* Singleton
Limopsidae	*Limopsis rupestris* sp. nov.
Pinnidae	*Pinna* sp.
Pteriidae	*Electroma* sp.
Propeamussiidae	*Parvamussium* sp.
Anomiidae	*Anomia* sp.
Limidae	limid
Gryphaeidae	*Pycnodonte (Phygraea)* sp.
Trigoniidae	*Eotrigonia paleocenica* Darragh

Lueinidae	*Jagolucina*? sp.
	lucinid A
	lucinid B
	Myrtea faseolata sp. nov.
Thyasiridae	*Thyasira* sp.
Ungulinidae	*Felaniella (Zemysia)* sp.
Eryeinidae	*Borniola* sp.
Cyamiidae	*Cyamiocardium silicula* sp. nov.
Astartidae	*Astarte (A.) notialis* sp. nov.
Carditidae	*Venericardia (Rotundicardia) petraea* sp. nov.
	Carditellopsis bellissima sp. nov.
Lahilliidae	*Lahillia australica* Singleton
Tellinidae	*Bertinella lapidaria* sp. nov.
Veneridae	*Dosinia (Dosinobia) saxatilis* sp. nov.
	Callistina (Tikia)? scopulensis sp. nov.
Corbulidae	*Caryocorbula* sp.
Hiatellidae	*Panopea* sp.
Cuspidariidae	*Cuspidaria* sp.
Verticordiidae	*Verticordia* sp.

Table showing numbers of specimens used in this study.

Limopsis rupestris sp. nov.	394
Astarte (A.) notialis sp. nov.	319
Ledina paucigradata Singleton	288
Bertinella lapidaria sp. nov.	114
Cucullaea psephea Singleton	94
Venericardia (Rotundicardia) petraea sp. nov.	82
Anomia sp.	81
Dosinia (Dosinobia) saxatilis sp. nov.	65
Cyamiocardium silicula sp. nov.	64
Carditellopsis bellissima sp. nov.	51
Lahillia australica Singleton	42
Eotrigonia paleocenica Darragh	31
Lamellinucula pyrenoides sp. nov.	28
Neilo (Australoneilo) cultrata sp. nov.	24
Callistina (Tikia)? scopulensis sp. nov.	15
Myrtea faseolata sp. nov.	13
Comitileda sp.	11
Jagolucina? sp.	10
Electroma sp.	7
Parvamussium sp.	7
Caryocorbula sp.	6
Pycnodonte (Phygraea) sp.	6
Verticordia sp.	4
Cuspidaria sp.	4
lucinid B	4
Pinna sp.	4
Panopea sp.	4
limid	3
Thyasira sp.	2
Felaniella (Zemysia) sp.	2
Borniola sp.	1
lucinid A	1
Total	1718

TROPHIC COMPOSITION

A valid trophic analysis of the fauna is not possible, because of the problems associated with collecting an unbiased sample. However, notwithstanding these problems, some broad generalisations can be made. It will be seen by comparing the numbers of individuals given above with the generalised groupings below, that the fauna as a whole is dominated by infaunal, suspension feeding bivalves with a significant infaunal, deposit feeding component. Three infaunal species comprise well over half (62%) the number of specimens. This pattern of composition suggests very shallow water. Nuculanids, tellins and astartids are very common elements in Recent northern hemisphere, cool shallow-waters (Thorson 1957), but *Limopsis* does not seem to have been recorded as a common element in association with them. Attempts to compare a Palaeocene assemblage from the southern hemisphere with Recent faunas of the northern hemisphere, or any other Recent fauna, should be treated with caution, because of the great difference in time and space. Also two of the most common elements in the Pebble Point fauna, *Limopsis* and *Astarte*, have living representatives which are eurybathyal. *Limopsis aurita* occurs from 38 to 3175 m and *Astarte sulcata* from 10 to 2000 m (Ekman 1967).

Generalised grouping of species according to feeding type and habitat

Infaunal deposit feeding:
Lamellinucula pyrenoides sp. nov., *Comitileda* sp., *Ledina paucigradata* Singleton, *Neilo (Australoneilo) cultrata* sp. nov., *Bertinella lapidaria* sp. nov., *Verticordia* sp.

Infaunal suspension feeding:
Cucullaea psephea Singleton, *Limopsis rupestris* sp. nov., *Eotrigonia paleocenica* Darragh, *Jagolucina*? sp., lucinid A, lucinid B, *Myrtea faseolata* sp. nov., *Thyasira* sp., *Felaniella (Zemysia)* sp., *Borniola* sp., *Cyamiocardium silicula* sp. nov., *Astarte (A.) notialis* sp. nov., *Venericardia (Rotundicardia) petraea* sp. nov., *Carditellopsis bellissima* sp. nov., *Lahillia australica* Singleton, *Dosinia (Dosinobia) saxatilis* sp. nov., *Callistina (Tikia)? scopulensis* sp. nov., *Caryocorbula* sp., *Panopea* sp.

Semi-infaunal byssate, suspension feeding:
Pinna

Epifaunal, byssate, suspension feeding:
Electroma sp., *Parvamussium* sp., *Anomia* sp., limid.

Epifaunal, attached, suspension feeding:
Pycnodonte (Phygraea) sp.

Infaunal carnivore:
Cuspidaria sp.

PREDATION

Countersunk boreholes (total 57) are present on 54 of the 1781 specimens studied. The holes were probably bored by a small species of naticid gastropod present in the fauna. Most of the holes (82%) were bored into 44 specimens of *Astarte (A.) notialis* sp. nov. One specimen had two uncompleted holes, a second had one uncompleted and one completed hole and a third specimen had two completed holes. All other bored *Astarte* had only one borehole. Other completed holes were found on specimens of *Jagolucina*? (3), *Cyamiocardium silicula* sp. nov. (3), *Carditellopsis bellissima* sp. nov. (3), and *Bertinella lapidaria* sp. nov. (2).

TEMPERATURE

It is only possible to give a very general indication of the water temperature in which the fauna lived. The fauna as a whole is similar to northern hemisphere Boreal faunas (see below) which presumably lived in cool temperate water. There are no genera present which are found in the warm-water faunas of the Paleocene of Africa and Asia. Species of genera such as *Myrtea*, *Thyasira*, *Felaniella*, *Borniola*, and *Carditellopsis* are found living in cold to warm temperate waters off eastern Australia.

RELATIONSHIPS WITH OLDER
AUSTRALIAN FAUNAS

The only Late Cretaceous fauna described from Australia is that from the Miria Formation, Carnarvon Basin, Western Australia (Darragh & Kendrick 1991). Given the geographical and stratigraphical separation of this fauna from that at Pebble Point, it could not be expected that they would have much in common and, indeed, only three genera in the Miria fauna might have provided an ancestor for Pebble Point genera: *Pycnodonte (Phygraea)*, *Panopea* and *Trigonia*. The first two are cosmopolitan genera and the Pebble Point representatives may easily have been derived from some other source, the Antarctic or New Zealand for instance. However, *Trigonia miriana* has many features similar to the Pebble Point *Eotrigonia paleocenica* and may belong to an ancestral group of the Pebble Point taxon (Darragh 1986).

RELATIONSHIPS WITH YOUNGER FAUNAS

Species of *Comitileda, Cucullaea, Limopsis, Pinna, Parvamussium, Anomia, Pycnodonte, Eotrigonia, Rotundicardia, Carditellopsis, Panopea, Cuspidaria* and *Verticordia* are found in Eocene rocks in the Otway Basin. Though most of the Eocene species do not seem to be closely related to the Paleocene species, the species of *Limopsis, Rotundicardia* and *Carditellopsis* do seem to be related. The species of *Comitileda*, however, does seem to be close to Oligocene and Miocene species and possibly represents the beginning of a lineage. Other than the Paleocene record, *Myrtea* is found from Pliocene to Recent, *Thyasira* is known from Middle Miocene to Recent and *Zemysia, Cyamiocardium* and *Borniola* are only known in the Recent fauna of Australia. It seems unlikely that the Paleocene species are directly related to the Miocene and living species, but species of the latter two genera are small to minute and too much emphasis should not be placed on their absence because such molluscs from the Australian Tertiary have been little studied.

Pebble Point genera not found above the Paleocene in Australia are *Lamellinucula, Ledina, Australoneilo, Astarte, Lahillia, Bertinella, Dosinobia* and *Caryocorbula*.

BIOGEOGRAPHY

An authoritative biogeographic analysis of the Pebble Point fauna is not yet possible because the generic placement of several of the species is doubtful. Equally the generic placement of many species described from other Paleocene faunas around the world is in doubt. Despite these problems some general conclusions can be made, however, as the taxonomy and relationships of Paleocene species become better known, modification will no doubt be required. It should also be emphasised that these conclusions are drawn from a study of the bivalves only and information from the gastropods may modify them.

Paleocene faunas are not particularly widespread throughout the world and some have not yet been the subject of modern revision, making comparison difficult. They fall into four very broad groupings.

1. An Early Paleocene Boreal fauna found in Europe extending from Denmark in the west as far east as the Volga Basin in Ukraine and possibly to Tashkent (Ravn 1939; Makarenko 1970; Anderson 1973, 1974). In the Late Paleocene, this fauna extended further south into the Anglo–Franco–Belgian Basin.

2. A temperate to warm-temperate fauna in the Early Paleocene found in Europe in Belgium and France (Glibert & Van der Poel 1973) and in America from New Jersey in the north as far south as Brazil (Gardner 1933). The Paleocene fauna of the United States Pacific coast could also be considered as part of this group (Zinsmeister 1983).

3. A tropical to warm water, Early to Late Paleocene Tethyan fauna extending from central west Africa and north Africa eastwards as far as India and Burma (Adegoke 1977).

4. A southern hemisphere group of faunas from isolated localities of varying ages in New Zealand (Finlay & Marwick 1937), Australia, Antarctica (Zinsmeister & Macellari 1988) and southern South America.

The first and third of the above groups are relatively homogeneous. The second group can be divided into an American subgroup of relatively homogeneous faunas and a European subgroup. The two subgroups have much in common (Gardner 1933).

The Pebble Point fauna has 10 genera, or about one third of the genera present, in common with group one. These genera are all regarded as cosmopolitan in cool to temperate waters. Many cosmopolitan or widely distributed genera are also shared with the second group. None of the Pebble Point genera, except the cosmopolitan genus *Pycnodonte (Phygraea)*, are shared with group three.

The only Paleocene faunas in the southern hemisphere are those at Pebble Point, the Wangaloan fauna of New Zealand; on the Antarctic Peninsula and in southern South America.

The Wangaloan fauna, a moderately diverse, shallow water fauna comprising about 20 genera is significantly older than that at Pebble Point, being early Teurian or Danian (Beu & Maxwell 1990). Faunas on the Antarctic Peninsula are also diverse and are of shallow water origin, but are either significantly older, Late Cretaceous ranging into the Early Paleocene, or much younger, Mid to Late Eocene (Zinsmeister & Macellari 1988; Stilwell & Zinsmeister 1992). Paleocene faunas in southern South America are so poorly known that a comparison has not been attempted.

At Pebble Point there are 32 bivalve taxa, of which only six seem to be related to taxa from the Wangaloan (*Ledina, Cucullaea, Electroma, Myrtea, Lahillia* and *Dosinobia*). The Pebble Point species of *Ledina, Cucullaea, Lahillia* and *Dosinobia* are close enough to the Wangaloan taxa to suggest that they are descended from them. A further three taxa (*Comitileda, Zemysia, Caryo-*

corbula) seem related to taxa from the Eocene of New Zealand.

Only five taxa seem to be related to Antarctic forms; *Australoneilo, Cucullaea, Pinna, Lahillia* and *Panopea*. These taxa are related to both Late Cretaceous and Late Eocene Antarctic forms. Of these *Cucullaea* and *Lahillia* are shared with New Zealand. *Electroma* also occurs in the Late Eocene of Antarctica. However, *Cucullaea*, *Pinna* and *Panopea* are cosmopolitan genera and cannot be regarded as necessarily indicating a close relationship between faunas.

Both *Astarte* and *Cyamiocardium* occur in Antarctic living faunas. Except as recorded here, *Astarte* is not known living or fossil either in Australia or New Zealand. *Astarte* is considered a typical member of cool-water boreal faunas.

In general the Pebble Point bivalves suggest considerable isolation from other Paleogene faunas and lend little support to the idea that southern Australia, or at least the Otway Basin, was part of the late Cretaceous–early Tertiary Weddellian Province (Zinsmeister 1979). The only unequivocal Weddellian taxa present are *Lahillia* and *Neilo (Australoneilo)* which presumably had a circumpolar distribution. Other characteristic Weddellian taxa such as aporrhaids and struthiolariids are not present.

This comparative isolation of the Pebble Point fauna can be explained by the disposition of the Australian continent *vis-à-vis* Antarctica. Accepting the scenario as depicted by Frakes et al. (1987, Figs 8–13) and Veevers et al. (1991, Figs 6–8), it would seem that a narrow east-west seaway open to the west, but restricted or blocked in the east by the South Tasman Rise, existed between Australia and Antarctica from Cenomanian times through into the Paleocene. Circulation of water and hence migration or transport of larvae from the east would have been limited, thus preventing easy migration of taxa from the New Zealand region and the Antarctic Peninsula area. Most of the taxa present were representatives of cosmopolitan groups, whose larvae would have been pelagic and long-lived, allowing wide dispersal.

The fauna of the Maastrichtian Miria Formation is also dominated by cosmopolitan generic taxa (Darragh & Kendrick 1991; Darragh & Kendrick 1994) suggesting isolation of the Australian plate at that time. Apart from *Eotrigonia*, endemic Australian bivalve taxa had not evolved by Paleocene time and it was not until the Late Eocene that endemic elements developed. By this time the fauna had also received an influx of new immigrants from the Tethyan and New Zealand regions and the basic

elements of the modern molluscan fauna were established (Darragh 1985).

TERMINOLOGY

The tooth notation used in the descriptions is that of Boyd & Newell (1969).

All specimens are housed in the Invertebrate Palaeontology Collection, Natural History Division, Museum of Victoria, register prefix NMV P.

Figured specimens were all whitened before being photographed.

SYSTEMATICS

Family NUCULIDAE

Lamellinucula Schenck, 1944

Type species. *Nucula tamatavica* Odhner, 1943, Recent, Madagascar.

Lamellinucula pyrenoides sp. nov.

Fig. 1J, N, Q, T

Description. Shell of small size (4–5 mm), ovate, strongly inequilateral, equivalve, moderately inflated, opisthogyrate, umbo situated about $1/4$ to $1/5$ from posterior end, valves slightly flattened to depressed on posterior flank. Lunule very narrow, barely developed. Escutcheon very narrow. Sculpture of 21 to 39 fine, sharp, commarginal ribs, slightly narrower than interspaces and on some specimens with a thin anastomosing riblet between some ribs. End of ribs at anterior margin against escutcheon somewhat thicker. Inter-rib spaces with fine, close spaced, radial costae. Sculpture begins about 1 mm from umbo; anterior to this valve is smooth. Muscle scars subcircular. Hinge with 7 posterior and 13 anterior teeth. Resilifer directed forwards, not projecting. Internal valve margin with fine denticulations.

Dimensions

Holotype P142956	L 5.1	H 4.1	T 3.0 (pr)
Paratype P142957	4.2	3.5	

Type material. Holotype P142956, collected T. A. Darragh, 17 February 1981; Paratype P142957, collected T. A. Darragh, 24 November 1992.

Type locality. PL3003.

Occurrence and material. PL3003 (27 specimens), PL3004 (1 specimen).

Remarks. There is nothing quite like this taxon in the Australian Eocene, though species which may possibly belong in the genus occur in the Oligocene

and Miocene. The genus has a cosmopolitan distribution and is known from the Paleocene of Europe, Asia and North America. There is nothing like it recorded from the early Tertiary of New Zealand or the Antarctic.

There is possibly another species of nuculid present represented by one specimen with a smooth valve surface and denticulate internal ventral margin. It is triangular in shape rather than oval. Also present are 16 very small (0.8–1 mm) specimens that are thick shelled, tumid and triangular with a smooth external valve surface and smooth internal ventral margin. It is not clear if these specimens are juveniles of the smooth species or represent yet another species of nuculid, possibly an *Austronucula*.

Family NUCULANIDAE

Comitileda Iredale, 1924

Type species. *Leda miliacea* Hedley, 1902, Recent, New South Wales.

Until a proper revision of the small rostrate nuculanids is undertaken, I follow Maxwell (1992) in using this genus rather than *Ledina* to which Australian species have been previously assigned. The genus occurs in New Zealand from Middle Eocene to Recent and in Australia from Paleocene to Recent.

Comitileda sp. cf. C. brachyryncha Maxwell, 1992

Fig. 1K–M

Description. Shell small (2–3 mm), ovate, almost equilateral, somewhat tumid, slightly rostrate at posterior end. Umbo central, projecting slightly, very slightly opisthogyral. Anterior dorsal margin gently convex; anterior margin strongly convex, merging into convex ventral margin; ventral margin gently convex, concave where it merges with the posterior margin; posterior dorsal margin straight; posterior margin short, strongly convex. Surface of valve smooth except for growth ridges. Hinge with 10 posterior and 8 anterior chevron-shaped teeth, apex directed towards umbo. Muscle scars subequal, barely visible; pallial line with shallow rounded sinus. Internal valve margin smooth.

Dimensions
Figured specimen P142863   L 2.7   H 1.9
Figured specimen P143862   2.2   1.4

Figured material. Figured specimen P142863, collected T. A. Darragh, 8 March 1977; Figured specimen P142862, collected T. A. Darragh, 22 November 1993.

Occurrence and material. PL3003 (11 specimens).

Remarks. One specimen is a pair with a countersunk gastropod drill hole in the right valve.

This species bears a very close resemblance to *Comitileda brachyryncha* Maxwell, Eocene, New Zealand and also to *C. praelonga* Tate, Oligocene to Miocene, Australia. The latter is more rostrate, slenderer and more pointed at the posterior end, but the differences are slight. It is more tumid than *C. miliacea* but is not as elongate and the umbo is not so opisthogyral. *Leda rhamphidia* Cossmann, Paleocene, Belgium is somewhat similar in shape to *C. miliacea*.

Ledina Dall, 1898

Type species. *Leda smirna* Dall, 1898 (= *Leda eborea* Conrad, 1860 non Conrad, 1846), Eocene, United States of America.

Ledina paucigradata (Singleton, 1943)

Fig. 1H–I, O–P, R–S, U–V

Nuculana paucigradata Singleton, 1943: 268, pl. 12, fig. 1a, b.

Description. Shell solid of medium to large size for genus (10–14 mm), elongate-ovate, posteriorly rostrate, equivalve, moderately inflated, umbones low, situated at about $\frac{1}{3}$ distance from anterior border. Anterior dorsal margin straight, merging into the strongly convex anterior margin; ventral margin regularly and gently curved, abruptly merging into posterior margin; posterior margin short, in some specimens rounded to blunt point; posterior ventral margin slightly convex, abruptly truncated by posterior margin.

Surface of valves sculptured with fine growth striae only.

Hinge with 10–14 anterior teeth, chevron shaped, pointed toward umbo, becoming weaker toward umbo; 19–23 posterior chevron shaped teeth, becoming straighter and vertically aligned toward umbo. Small triangular resilifer between anterior and posterior tooth series.

Anterior muscle scar laterally elongated; posterior scar vertically elongate. Pallial sinus shallow, wide, usually not visible. Internal margins of valves smooth.

Dimensions
Holotype P127990	L 11	H 6	T 2
Figured specimen P142961	14	7	2.3 LV
Figured specimen P142962	12	7	2.3 RV
Figured specimen P142960	11	6	4.5 Pair
Figured specimen P142963	12	6	6.6 Pair

Types. Holotype P127990 (MUGD 1868), left valve, collected G. Baker, January 1942. The holotype has
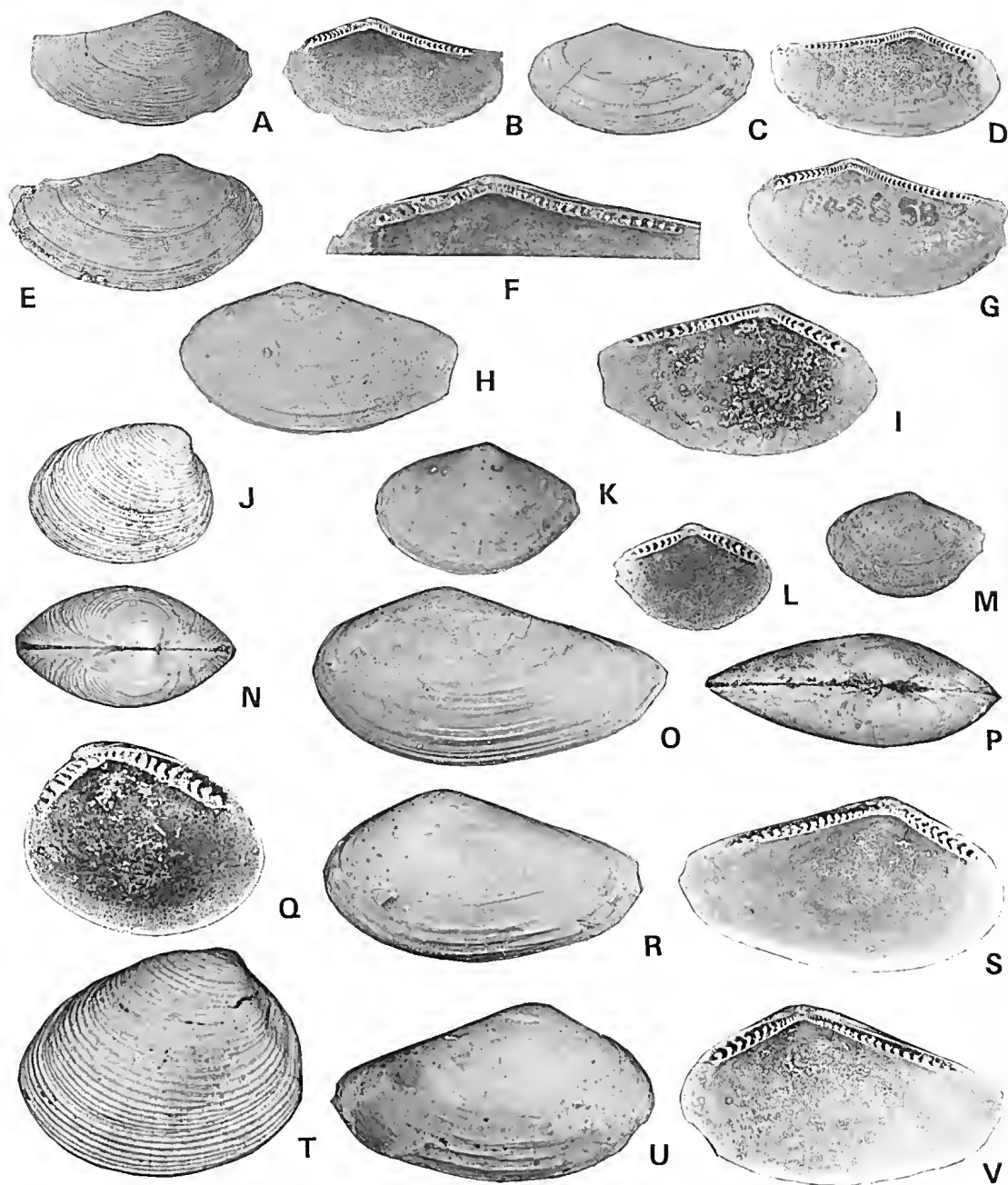
Fig. 1. A–G, *Neilo (Australoneilo) cultrata* sp. nov. A–B, NMV P142861, paratype, PL3003, ×1.8. C–D, NMV P142859, paratype, PL3003, ×1.8. E, G, NMV P142858, holotype, PL3003, ×1.5. F, NMV P142860, paratype, PL3003, ×3.5. H–I, O–P, R–S, U–V, *Ledina paucigradata* (Singleton). H–I, NMV P127990, holotype, second point NW of Pebble Point, ×3.5. O, NMV P142961, PL3003, ×3.5. P, NMV P142960, PL3003, ×3.7. R–S, U–V, NMV P142963, pair, PL3003, ×3.75. J, N, Q, T, *Lamellinucula pyreuoides* sp. nov. J, NMV P142957, paratype, PL3003, ×6.2. Q, NMV P142957, ×8.1. N, NMV P142956, holotype, PL3003, ×6.1. T, NMV P142956, holotype, ×9.6. K–M, *Comitileda* cf. *C. brachyryncha* Maxwell. K, NMV P142862, PL3003, 13. L–M, P142863, PL3003, ×8.1.

approximately one millimetre broken off the posterior end. Figured specimens, P142960, P142961, P142962, collected T. A. Darragh, 8 March 1977; Figured specimen P142963, collected T. A. Darragh, 27 November 1972.

Type locality. Coastal cliffs 2½ miles south-east of Princetown, Victoria, second point north-west of Pebble Point (= PL 3004).

Occurrence and material. PL3001 (14 specimens), PL3003 (240 specimens), PL3004 (34 specimens).

Remarks. This is one of the most common molluscs in the fauna. Paired valves are very uncommon. *L. paucigradata* is very similar in overall features to the New Zealand Paleocene *L. taioma* (Finlay & Marwick 1937), but is more elongate, the umbo is not so centrally situated and the anterior dorsal margin is straight rather than concave as in *L. taioma.*

Compared with the type species of the genus, *L. smirna* Dall (Gardner 1933), *paucigradata* is more elongate and not so equilateral. Both *L. fresnoensis* (Dickerson) and *L. duttonae* (Vokes) (Paleocene and Eocene of California) have better developed lunules and escutcheons (Moore 1983).

Darragh (1985) recorded *L. paucigradata* from the Rivernook Member of the Dilwyn Formation. Collection of better preserved material shows that the determination was in error.

Apart from the occurrence here, the genus is known only from the Paleocene to Eocene of New Zealand and North America.

Neilo (Australoneilo) Zinsmeister 1984

Type species. Australoneilo rossi Zinsmeister, 1984, Late Eocene, Antarctica.

Zinsmeister (1984) distinguished *Australoneilo* from *Neilo* by the absence of commarginal ribbing and by it having a poorly developed rostrum. These differences are slight, particularly as some species of *Neilo* have obsolescent ribbing, so subgeneric status seems appropriate. *Australoneilo* may be distinguished by its more prominently curved rather than almost straight ventral margin and by the lack of a prominent umbo to posterior ventral margin ridge. *Neilo* also has a prominently rectangular truncated posterior margin.

Neilo (Australoneilo) cultrata sp. nov.

Fig. 1A–G

Description. Shell of small size for subgenus (18–21 mm), narrow, elongate, subquadrangular, moderately swollen medially and tapering gently posteriorly. Umbo small, slightly projecting, orthogyral, situated about ⅓ valve length from anterior end. Anterior margin somewhat sharply rounded; anterior dorsal margin concave; posterior dorsal margin concave, abruptly truncated by posterior margin; ventral margin long, gently convex. Posterior umbonal ridge ill defined.

Lunule very narrow and weak. Escutcheon narrow, extending to posterior margin, sharply defined by ridge. One or two shorter ridges within escutcheon.

Sculpture consisting of 8 to 14 widely spaced, somewhat irregular, thin, commarginal riblets extending to about 2.5–3 mm from beak, present on central flank but not present on posterior or anterior flanks. Remainder of valve sculptured with growth increments only.

Hinge with chevron shaped teeth with apices directed toward umbo, becoming thinner and straightening toward beak and meeting under it. 15 to 19 anterior teeth and 22 to 29 posterior teeth. No resilifer.

Pallial sinus wide, moderately deep, extending about halfway between umbo and posterior border, sloping gently ventrally. Muscle scars barely visible, small, oval; anterior elongated dorso-ventrally; posterior elongated laterally. Internal valve margin smooth.

Dimensions

Holotype P142858	L 21	H 11	T 3.5
Paratype P142859	18	9	3
Paratype P142861	17	9	3.5

Type material. Holotype P142858, left valve; Paratype P142859, right valve, collected T. A. Darragh, 27 November 1977; Paratype P142861, right valve, collected T. A. Darragh, 13 November 1984.

Type locality. PL3003.

Occurrence and material. PL 3001 (6 specimens); PL 3003 (14 specimens); PL3176 (3 specimens); PL3177 (1 specimen). 2125–2131 feet, Kaladbro 2 bore (1 specimen); Mersey Valley Oil Co., 1926; Mumbannar no. 1, 1492–1502 feet, 37°5'37"S,141°03'19"E, 4 km NE of Mumbannar (2 specimens).

Remarks. In outline this species is very close to the type species, *N. (A.) rossi,* but is about half the size, slightly narrower and more elongate and has riblets on the umbo. *N. (A.) gracilis* (Wilckens 1907), Late Cretaceous–Paleocene, Southern Patagonia and Seymour Island and *N. (A). casei* Zinsmeister & Macellari 1988, Paleocene, Seymour Island both lack the fine umbonal ribs of *N. (A.) cultrata* and are not so elongate.

The subgenus was previously known only from the Late Cretaceous, Paleocene and Eocene of Antarctica and South America.
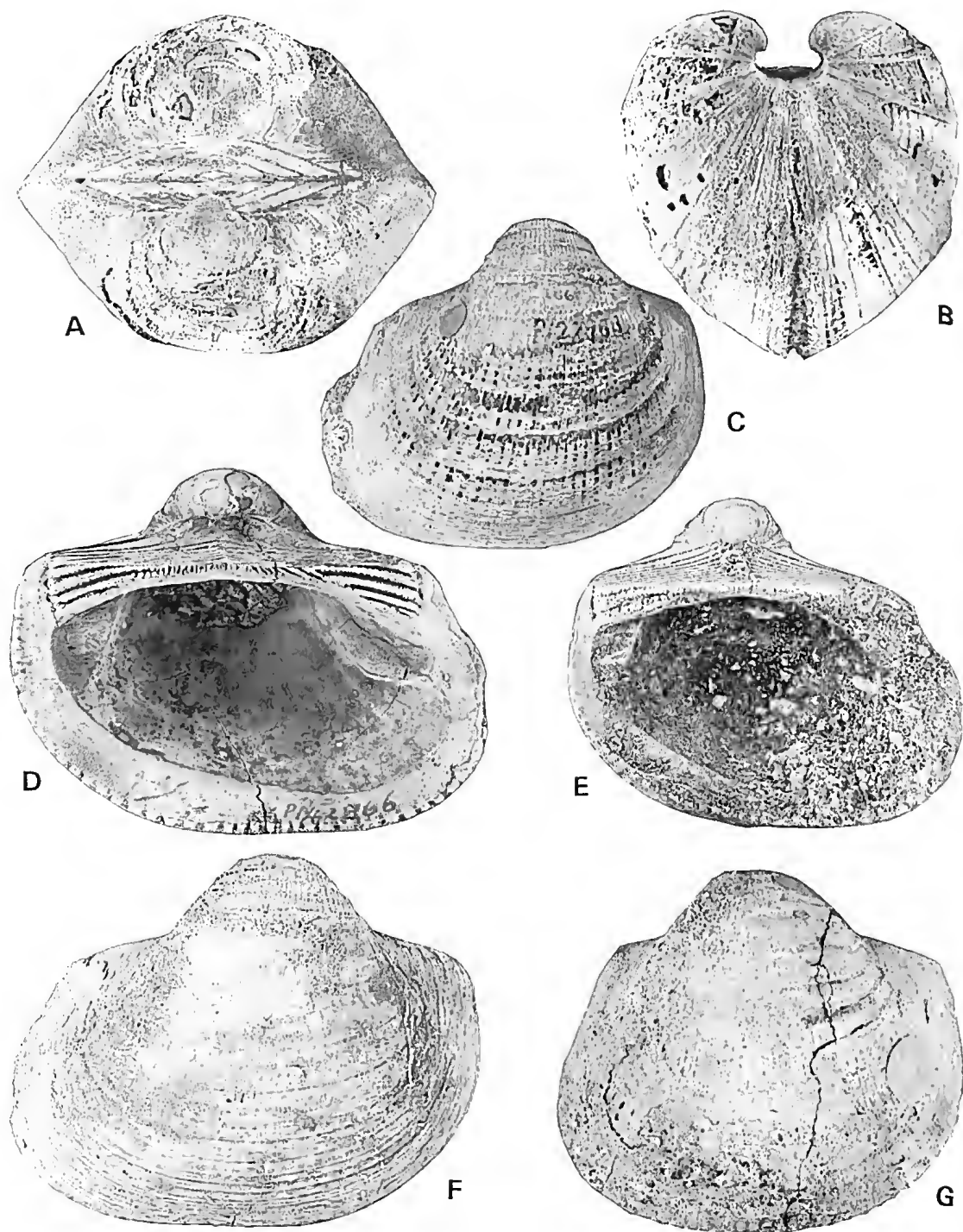
Fig. 2. A–G, *Cucullaea psephea* Singleton. A–B, NMV P142865, PL3004, ×1.2. C, E, NMV P127953, holotype, second point NW of Pebble Point, ×1. D, F, NMV P142866, PL3004, ×1.2. G, NMV P127954, paratype, second point NW of Pebble Point, ×1.

Family CUCULLAEIDAE

Cucullaca Lamarck, 1801

Type species. *Arca cucullata* Röding, 1798, Recent, Indo-Pacific.

Genera of the *Cucullaea* group are in need of revision, so I have placed *psephea* in *Cucullaea (sensu lato)*. Either *Cucullona* Finlay & Marwick 1937 or *Latiarca* Conrad 1862 could be used if it was thought that there is sufficient justification to separate one or the other from *Cucullaea*. The hinge is similar to species of *Idonearca*, Late Cretaceous and Paleocene of North America, but the species in that genus all lack marginal denticulations.

Davies (1929) pointed out that *Cucullaea* was typical of the Boreal Paleocene of Europe and North America and the Paleocene of southern South America, i.e. that it had a bipolar distribution, and that it was absent from the Tethyan faunas of Africa and Asia. (See also Davies 1934, Fig. 9.) The Australian occurrence fits in with this pattern of distribution. The Recent distribution of *Cucullaea* is temperate to tropical. The Paleocene distribution should provide a note of caution in using the occurrence of *Cucullaea* in a fauna as evidence for warm water.

Cucullaea (s.l.) psephca Singleton, 1943

Fig. 2A–G

Cucullaea (Cucullona) psephea Singleton 1943: 269, pl. 13, figs 7a–b, 8a–b. — Ludbrook 1973: pl. 24, figs 1, 3.

Description. Shell of medium size for the genus (60×47–35×32), thick, inequilateral, equivalve, strongly inflated, subquadrate, with large prominent incurved umbos. Radial sulcus running from umbo to posterior sinus situated at upper part of posterior margin. Exterior of valves almost smooth, sculpted with fine growth lines, somewhat undulose towards margin where they cross very faint radial ribs. When weathered, surface shows radial elements aligned with internal margin denticulations.

Ligamental area triangular, elongate with 7 to 12 deeply incised chevron grooves. Hinge heavy with subhorizontal, thick, grooved teeth at each end of hinge and with numerous coarse denticulations between the two groups of teeth. Three anterior teeth and in some specimens a weak fourth ventrally. Four to six posterior teeth on posterior side of left valve.

Adductor scars large, prominent. Anterior D shaped, somewhat vertically elongated. Posterior D shaped, elongated laterally with prominent myophoric ridge ventrally.

Pallial line deeply incised. Internal margin coarsely denticulate.

On unweathered juvenile specimens, ubonal region sculptured with very narrow widely spaced ribs that correspond to the marginal denticulations. These flatten out and become less perceptible on mature specimens.

Dimensions

Holotype P127953	L 59	H 51	VTh 27
Paratype P127954	40	36	15
Figured specimen P142865	52	44	42 pair
Figured specimen P123866	60	49	26

Type material. Holotype P127953 (MUGD 1869), right valve, Paratype P127954 (MUGD 1870), right valve, collected G. Baker, January 1942. Figured specimens P142865–6, PL3004, collected T. A. Darragh, 19 November 1970.

Type locality. Coastal cliffs $2\frac{1}{2}$ miles south-east of Princetown, Victoria, from second point north-west of Pebble Point ($=$ PL 3004).

Occurrence and material. PL3001 (29 specimens), PL3003 (28 specimens), PL3004 (37 specimens), PL3005 (7 specimens), PL3006 (1 specimen).

Remarks. Nearly all mature specimens are decorticated to some extent. As Singleton has pointed out, this species is very close to *Cucullaea inarata* Finlay & Marwick from Wangaloa. The sculpture is identical and the outline similar. *C. psephea* has more incurved umbos and hence is a little wider across the valves. A larger range of the former for comparison may show that the differences between the two are not consistent and that *Cucullaea psephea* is a synonym of *C. inarata*.

It is somewhat similar in sculpture to *C. ellioti* Zinsmeister & Macellari, Paleocene, Antarctica and to *C. antarctica* Wilckens, Late Cretaceous, Antarctica and Argentina, but these are not so equilateral as *C. psephea*. It is also close to *C. gigantea* Conrad, Paleocene, eastern United States of America but seems to be not so strongly ribbed.

Cucullaea psephea is closer to the other Southern Hemisphere species than to those of the Northern Hemisphere which mostly bear weak to strongly developed radial ribs.

Family LIMOPSIDAE

Limopsis Sassi, 1827

Type species. *Arca aurita* Brocchi, 1814, Pliocene, Italy.
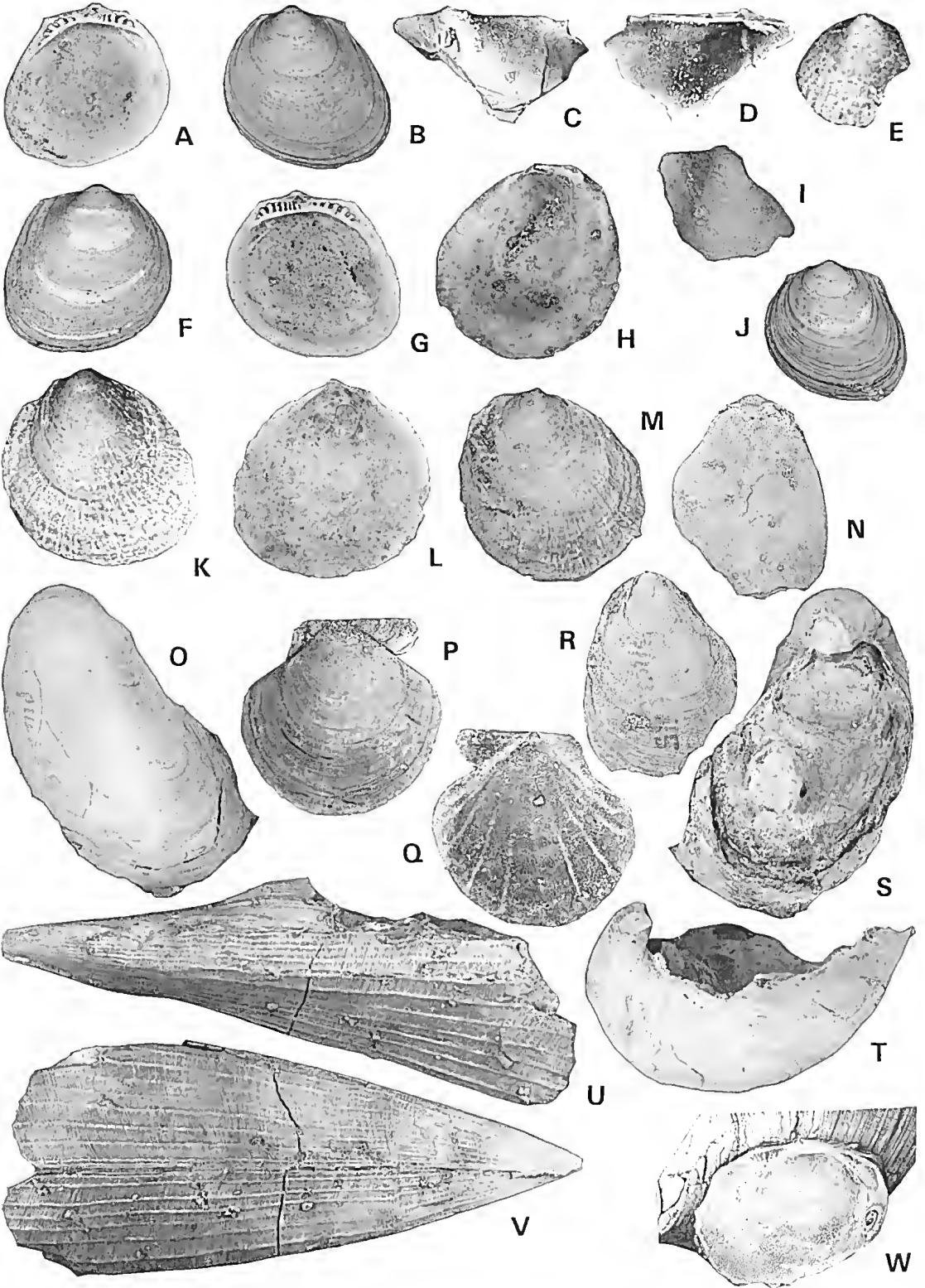
Limopsis rupestris sp. nov.

Fig. 3A–B, F–G, J

Limopsis sp. nov. Singleton 1943: 271, pl. 12, fig. 2a, b.

Description. Shell roundly subquadrate, slightly oblique, of small to medium size (7×7–10×11) for the genus, solid, equivalve, moderately convex, inequilateral. Umbos small, pointed, extending beyond dorsal margin. Posterior and anterior dorsal margins short, straight; posterior margin straight or slightly concave; ventral margin convex, merging imperceptably into anterior margin; anterior margin convex.

Hinge strongly arched; cardinal area triangular, low elongate with central triangular ligament pit encroaching slightly onto central hinge teeth. Right valve with 4 to 6 strong posterior teeth and 3 or 4 weak teeth in centre and 4 to 5 strong anterior teeth. Left valve with 4 to 6 strong posterior teeth, 2 to 3 weak teeth in centre and 4 to 5 strong anterior teeth.

Anterior muscle scars bounded ventrally by sharp ridge, small and obliquely elongated; posterior scar much larger, subtriangular. Internally valves radially striated to the pallial line. Internal valve margin smooth.

Surface of valve shiny, sculptured only with irregular growth striae and very faint (worn off on most specimens) radial striae.

Dimensions

Holotype P142871	L 7.2	H 7.2	T 2
Paratype P142872	7.5	7.5	2.5
Paratype P142873	6	6.5	2

Types. Holotype P142871, Paratypes P142872-3, collected T. A. Darragh, 27 November 1972.

Type locality. PL3003.

Occurrence and material. PL 3001 (38 specimens), PL 3003 (322 specimens), PL 3004 (34 specimens).

Remarks. This is one of the most common bivalves in the fauna. The outer surface of the valves is worn in most specimens. Articulated pairs are very rare. It is somewhat similar to *Limopsis chapmani* Singleton, Late Eocene and Oligocene of south-eastern Australia, particularly to the ecomorphs of that species from the Browns Creek Clay, but the radial elements in *chapmani* are much stronger than those of *rupestris*. However, the latter may well be ancestral to the former.

It is quite unlike the New Zealand Paleocene *L. microps* (Finlay & Marwick 1937) which looks almost like a species of *Glycymeris*. *L. rupestris* is almost twice the size, oblique in shape and not almost equilateral as in the former. *L. antarctica* Wilckens, Late Cretaceous, Seymour Island is twice the size, more rounded and oblique in shape.

It seems similar to *L. ludbrookae* Glibert & Van der Poel, Paleocene, Europe, but that species is not so oblique, and also to *L. obesa* Ravn, Danian, Faxe, but that species is more rounded in outline.

There seems to be nothing similar recorded from North or South America.

Family PINNIDAE

Pinna Linnaeus, 1758

Type species. *P. rudis* Linnaeus, 1758, Recent, Atlantic.

Pinna sp.

Fig. 3U–V

Description. Shell large (158 + mm), thin, wedge-shaped, equilateral, with a median carina giving a rhomboid cross section. Sculpture consisting of fine radial costae, much narrower than interspaces, becoming broader posteriorly; left valve with 11 to 12 ribs (8 ribs on dorsal side of median carina) plus wavy irregular ribs on anterior ventral portion of valve. Right valve with 11 ribs (7 ribs on dorsal side of median carina). Internal features of valves not visible.

Figured material. Figured specimen P142868, collected T. A. Darragh and D. J. Holloway, 23 November 1992.

Occurrence and material. PL3003 (2 specimens), PL3004 (1 specimen), PL3176 (1 specimen).

Remarks. There are four specimens available; a large, slightly crushed pair, 158 + mm in length (P142868); a fragmentary pair (P142869, length 96 mm), a fragmentary right valve (P142870) and a fragmentary valve.

Fig. 3. A–B, F–G, J, *Limopsis rupestris* sp. nov. A–B, NMV P142871, holotype, PL3003, ×3.5. F–G, NMV P142872, paratype, PL3003, ×3.5. J, NMV P142873, paratype, PL3003, ×3.6. C–D, I, *Electroma* sp. C–D, NMV P142965, PL3003, ×6.4. I, NMV P142966, PL3003, ×6.6. E, limid. NMV P142881, PL3003, ×7.5. H, K–M, *Anomia* sp. H, M, NMV P142878, PL3003, ×3.6. K–L, NMV P142879, PL3003, ×3.4. N–O, R–T, W, *Pycnodonte (Phygraea)* sp. N, R, NMV P142885, PL3004, ×1.8. O, S–T, NMV P142887, PL3001, ×1.5. W, NMV P1142888, PL3003, ×1. P–Q, *Parvamusium* cf. *P. hauniense* Ravn. NMV P142874, PL3003, ×1.6. U–V, *Pinna* sp. NMV P142868, PL3004, ×0.6.

As far as comparison is possible on the basis of this limited material, it is very similar in morphology to *Pinna sobrali* Zinsmeister, Late Eocene, Meseta Formation, Seymour Island and also to *P. burrowsi* Dickerson, Late Paleocene, California. Fragmentary specimens of a pinnid from the Late Oligocene Jan Juc Formation, Torquay, seem to be more hatchet-shaped rather than wedge-shaped and probably belong in *Atrina*.

Family PTERIIDAE

Electroma Stoliczka, 1871

Type species. *Avicula smaragdina* Reeve, 1857, Recent, Indonesia.

Pterelectroma Iredale 1939: 332.

Electroma sp.

Fig. 3C–D, 1

Description. Shell small (juveniles), thin, nacreous, oblique; anterior with a triangular wing separated from flank of valve by slight sinus. Umbo projecting slightly above hinge line, opisthogyral. Hinge long and straight with triangular posteriorly directed resilifer pit under umbo, slightly anterior of mid point of hinge. Hinge with long posterior lateral and one very short anterior lateral. Internal features of valve not preserved. External surface of valve smooth.

Dimensions
Figured specimen P142966   L 1.4   H 1.2
Figured specimen P142965   4.5 +   2.5 +

Figured material. Figured specimens P142965–6, collected T. A. Darragh, 24 November 1992.

Occurrence and material. PL3003 (7 left valves).

Remarks. All five specimens are small and the two smallest are almost certainly juveniles. Only two valves are sufficiently complete and large enough for comparison with other taxa. It seems similar to Paleogene species assigned to *Electroma* Stoliczka, though *Pteria* has also been used for such species and may well be the correct taxon.

The anterior of the valve is slightly more produced than in juveniles of *Electroma georgiana* (Quoy & Gaimard), living, southern Australia and the central part of the valve is much more convex (higher). In this respect it is somewhat similar to *Electroma zebra* (Reeve), Recent, Queensland, type species of *Pterelectroma* Iredale, 1939. *Pterelectroma* was separated from *Electroma* on the basis of the former being smaller and thinner and having a definite posterior wing separated from the body. Comparison of specimens of *E. zebra* and *E. georgiana* shows that the development of the posterior wing is highly variable in both species and this cannot be used as a generic character to separate *Pterelectroma*.

In shape the Pebble Point species is similar to *Electroma stampinensis* (Deshayes), Early Oligocene, Europe, but is not so oblique as other Eocene taxa assigned to *Electroma* by Glibert & Van der Poel (1965). It has a smaller anterior wing and is more rectangular in shape than *E. intecta* Finlay & Marwick, Wangaloan, New Zealand. *E. notiala* Stilwell & Zinsmeister, Late Eocene, Seymour Island, is much more oblique than the Pebble Point taxon. Despite the difficulty of determination of the Pebble Point material, it is clear that the Pebble Point taxon belongs to a group that was widespread in the early Paleogene.

Family PROPEAMUSSIIDAE

Parvamusium Sacco, 1897

Type species. *Pecten duodecimlamellatum* Bronn, 1831, Miocene, Italy.

Parvamusium sp. cf. P. hauniense Ravn, 1939

Fig. 3P–Q

Description. Shell small, thin, subcircular in outline, flat. Right ears unequal, with byssal notch in anterior ear. Sculpture of left valve consisting of very fine, regular, closely spaced, shallow grooves; right valve worn, all traces of sculpture removed. Internally sculptured with widely spaced, high, narrow radial costae extending almost to valve margin (10 in RV and 8 in LV).

Dimensions
Figured specimen P142874   L 8.5   W 8.5 RV
Figured specimen P142875   5.8   6.0 LV

Figured material. Figured specimen P142874, collected T. A. Darragh, 13 November 1984.

Occurrence. PL3001 (1 specimen), PL 3003, (5 specimens), PL3004 (1 specimen).

Remarks. The left valve of *P. hauniense* Ravn, Paleocene of Denmark and Germany (Anderson 1973) is similar in shape and sculpture, however, the eroded condition of the right valve of the Pebble Point taxon precludes any close comparison with any other species in the genus.

Parvamusium occurs in the Paleocene in Europe and western and south-eastern United States. As yet there are no records from the Paleocene of New Zealand, Antarctica or South America. *P. atkinsoni* Johnstone of the Late Eocene to Middle Miocene of southern Australia has a similarly

sculptured left valve and a right valve with reticulate sculpture.

Family ANOMIIDAE

Anomia Linnaeus, 1758

Type species. *Anomia ephippium* Linnaeus, 1758, Recent, Europe.

Anomia sp.

Fig. 3H, K–M

Description. Shell small (8 × 10–13.5 × 14), thin, translucent, irregularly sub-circular to elliptical in outline, slightly higher than wide, inequilateral. Left valve moderately convex, sculptured with narrow, widely separated radial ribs. Umbo small, pointed. In most cases left valve margin leached away in front of umbo (byssal notch area?). Right valve flat, internal features not known. Left valve central white area elongate, individual muscle scars not visible owing to poor preservation. Small anterior pedal retractor scar visible. Umbonal area missing in most cases. Outer surfaces of most valves either worn or outer and inner surfaces leached away. A few specimens show coarse, beaded (scabrose?) radial ribs.

Dimensions
Figured specimen P142878   L 7.8   H 9   T 1.5
Figured specimen P142879   8.2   9   2

Figured material. Figured specimens P142878–9 collected T. A. Darragh, 2 December 1985.

Occurrence and material. PL3001 (53 specimens), PL3003 (28 specimens).

Remarks. The genus has a wide but patchy distribution in the early Tertiary, occurring in western and eastern Europe, eastern and western United States of America, Central America and New Zealand. Owing to the poor preservation, it is difficult to compare the Pebble Point specimens with those from other regions.

Family LIMIDAE

Limid indet.

Fig. 3E

Description. Shell small (2 + × 2.5 mm), equilateral?, oval, slightly higher than wide; umbo somewhat inflated, orthogyral, projecting very slightly above hinge margin; auricles small, subequal. Approximately 30 radial ribs, thin and crowded on anterior and posterior flanks, broad and widely spaced on central flank. Ligamental area, centrally situated, triangular; teeth if present,

not visible but some faint vertical striations present. Internal features of valves eroded.

Dimensions
Figured specimen P142881   L 2.4 (est.)   H 2.3 +

Figured material. Figured specimen P142881, collected T. A. Darragh, 24 November 1992.

Occurrence and material. PL3001 (1 specimen); PL3003 (1 specimen); PL3004 (1 specimen).

Remarks. The three specimens are all worn and fragmentary. One specimen is partly decorticated. Owing to the poor preservation of the three specimens, it is not possible to be certain of the generic placement. The taxon may be a *Limatula*, if it is edentulous; if not then a *Limea*, though it seems to be almost equilateral rather than produced anteriorly as in that genus. However, all specimens are probably juveniles and may not show the outline of the mature shell.

Family GRYPHAEIDAE

Pycnodonte (Phygraea) Vyalov, 1936

Type species. *Pycnodonte (Phygraea) pseudovesicularis* Gümbel 1861, Paleocene, Austria.

Pycnodonte (Phygraea) sp.

Fig. 3N–O, R–T, W

Description. Shell gryphaeiform, elongate, small for genus (34 × 25–39 × 21), slightly to strongly oblique, attachment area small to large; left valve highly inflated and incurved, with prominent commissural shelf on dorsal half of valve; chomata simple transverse bars, few on anterior side, close to hinge, many on posterior side extending along commissural shelf well away from hinge; sinus not very well developed. Right valve flat to slightly concave, with very weakly developed chomata. Sculpture of fine growth lines.

Dimensions
Figured specimen P142885   W 14   H 18
Figured specimen P142887   20   35
Figured specimen P142888   29   23

Figured material. Figured specimen P142885, collected T. A. Darragh, 20 October 1971; Figured specimen P142887, collected T. A. Darragh, 16 February 1981; Figured specimen P142888, collected T. A. Darragh, 24 November 1992.

Occurrence and material. PL3001 (1 specimen), PL3003 (2 specimens), PL3004 3 specimens.

Remarks. This species comes closest to specimens of *Pycnodonte (Phygraea)* sp. cf. *P. vesiculosa* (Sowerby, 1816) figured by Zinsmeister (1988) from
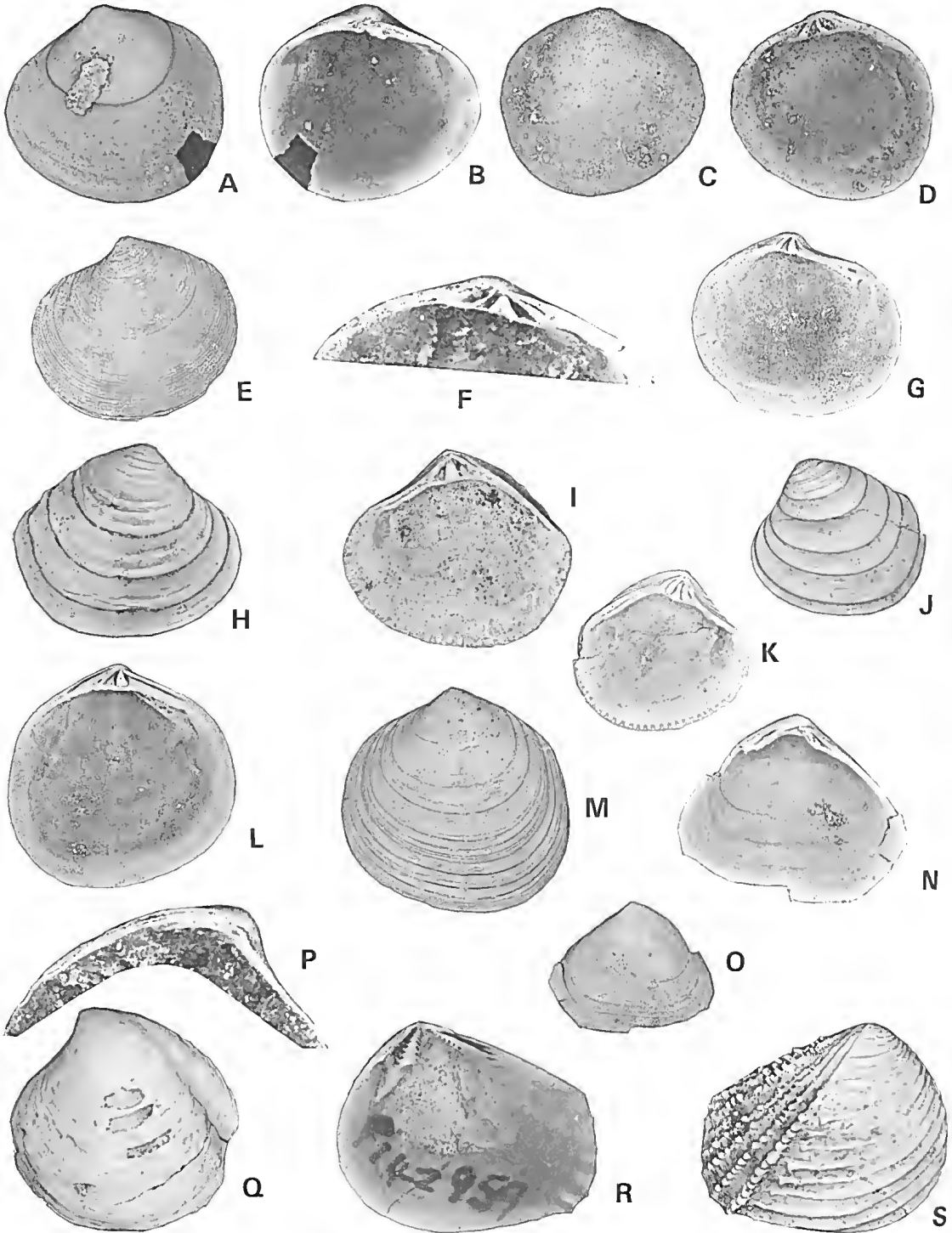
the Late Cretaceous of Seymour Island, Antarctica. Zinsmeister noted that his specimens lacked the radial posterior furrow typical of the species.

Somewhat similar specimens were figured by Panteleev (1974) as *Pycnodonte frauscheri* Traub from the Early Paleocene of the Mangyshlak district of the eastern side of the Aral Sea.

The Pebble Point taxon bears some resemblance to *Pycnodonte (Notostrea) tarda* (Hutton) Paleocene, New Zealand and *P. (N). lubra* (Finlay), Late Eocene, southern Australia, but it is narrower and more incurved, not so produced posteriorly and lacks the radial posterior furrow that separates the posterior from the rest of the valve.

Pycnodonte (Phygraea) has a cosmopolitan distribution ranging in age from Cretaceous to Miocene. Darragh & Kendrick (1991) discussed the Late Cretaceous and Paleocene representatives in north-west Western Australia, from which the Pebble Point taxon may be descended.

Two specimens from locality PL3003 are attached to other shells. P142888 is attached to the posterior flank of a right valve of *Lahillia australica*. The growth of the oyster suggests that it became attached after the valves of the *Lahillia* had become separated and the right valve lay on the bottom, rather than whilst the *Lahillia* was still living. The second oyster, P142889, is attached close to the ventral margin of a specimen of *Cucullaea psephea* and must have become attached after the death of the *Cucullaea*. P142888 has a few transverse barlike chomata on the commissural shelf close to the hinge. This specimen, though attached, seems similar in internal features to the three unattached specimens and I believe represents the same taxon. It is very similar to the specimen attached to a specimen of *Pycnodonte (Phygraea) seymourensis* figured by Zinsmeister (1988, Fig. 11.1).

Family TRIGONIIDAE

Eotrigonia Cossmann, 1912

Type species. *Trigonia semiundulata* McCoy, 1866 (= *T. subundulata* Jenkins, 1865).

Eotrigonia paleocenica Darragh, 1986

Fig. 4R–S

Eotrigonia paleocenica Darragh 1986: 10, Figs 4G, 1–L, N, 5A–B.

Dimensions
Figured specimen P142959 W 11 H 9

Figured material. Figured specimen P142959, collected T. A. Darragh, 2 December 1985.

Occurrence and material. PL3001, PL3003, PL3004.

Remarks. This taxon was fully described in the original description. Since then another 15 specimens have been collected which add nothing new to the concept of the species.

Family LUCINIDAE

Jagolucina Chavan, 1939

Type species. *Lucina concava* Defrance, 1823, Eocene, France.

Jagolucina ? sp.

Fig. 4E, G

Description. Shell subcircular, of average size (6–10 mm), moderately inflated; umbo pointed, prosogyral; anterior dorsal margin concave; anterior, ventral and posterior margins regularly convex, not differentiated from one another; posterior dorsal margin straight. Lunule short, prominent. Sculpture of fine, close-set, commarginal ribs.

Hinge: left valve with bifid anterior cardinal; thin posterior cardinal; two anterior laterals separated by short socket; possibly one posterior lateral.

Anterior muscle scar long, narrow, divergent from pallial line, extending from under anterior lateral tooth well into valve. Posterior scar lozenge-shaped, not clearly visible.

Internal margin of shell smooth.

Dimensions
Figured specimen P142890 L 6.5 H 6
Figured specimen P142891   11.2   10.5

Figured material. Figured specimen P142890, collected T. A. Darragh, 13 November 1984.

Fig. 4. A–D, F, *Cyamiocardium silicula* sp. nov. A–B, NMV P142904, paratype, PL3003, ×8.1. C–D, NMV P142902, holotype, PL3003, ×8.1. F, NMV P142903, paratype, PL3003, ×15. E, G, *Jagolucina* ? sp. NMV P142890, PL3003, ×4.75. H–K, *Astarte notialis* sp. nov. H–I, NMV P142900, holotype, PL3003, ×1.8. J–K, NMV P142901, paratype, PL3003, ×5. L–M, *Fellaniella (Zemysia)* sp. NMV P142897, PL3003, ×3.4. N–O, *Borniola* ? sp. N, NMV P142899, PL3003, ×8.5. O, NMV P142899, ×5.5. P–Q, *Thyasira* sp. P, NMV P142949, PL3003, ×6.75. Q, NMV P142949, ×4.5. R–S, *Eotrigonia paleocenica* Darragh. NMV P142959, PL3003, ×3.25.

Occurrence and material. PL3001 (one left valve), PL3003 (8 left and one right valve).

Remarks. All specimens are very worn and the generic position is very much open to doubt. Three of the left valves have gastropod boreholes. I have found no obviously related species in the southern hemisphere. *Jagolucina* occurs in the Paleocene and Eocene of Europe.

Lucinid indet. sp. A

This species is represented by a single right valve P142940, probably juvenile, measuring 2.3 × 2.0. The hinge is edentulous and there is a groove running from behind the umbo towards the posterior. Sculpture consists of growth lines only. It has not been possible to determine to what genus the taxon belongs. It is possibly an *Anodontia* or some other similar smooth edentulous lucinid.

Lucinid indet. sp. B

Description. Shell small (6.3 × 5.7–9.5 × 8.5 mm), weakly inflated; umbo small, pointed, orthogyral; posterior dorsal margin straight; posterior margin almost straight, somewhat truncating posterior dorsal margin; ventral and anterior margins convex, merging imperceptibly; anterior dorsal margin concave; lunule deeply sunken. Sculpture of widely separated, thin commarginal lamellae.

Hinge: left valve with strong triangular anterior cardinal; thin posterior cardinal separated from anterior cardinal by narrow triangular socket. Posterior laterals formed from valve margin (valve worn and not well preserved). Right valve with weak anterior cardinal? (worn); central triangular socket; posterior cardinal strong, blade-like; short, stout (worn) anterior and posterior laterals; short sockets dorsal to these.

Margins of valves smooth. Muscle scars and pallial line not observed.

Material. PL3001 (1 right valve); PL3003 (2 right valves); PL3004 (1 left valve).

Remarks. Owing to the limited nature of the material and its poor preservation it has not been possible to assign this species to a genus. Two specimens are incomplete and worn and the possibility exists that they do not belong in the same taxon as the others.

Myrtea Turton, 1822

Type species. *Venus spinifera* Montagu, 1803, Recent, Mediterranean.

Myrtea faseolata sp. nov.

Fig. A–G

Description. Shell small (4 × 3.5 mm–5 × 6.5), elongate, oval, moderately inflated; umbo small, pointed, situated at posterior third; posterior and anterior dorsal margins concave; posterior margin straight, abruptly truncating the posterior dorsal and ventral margins; anterior margin strongly convex, merging imperceptibly into ventral margin; ventral margin regularly convex. Sculpture of widely spaced, well developed commarginal lamellae, slightly frilled on anterior of flank.

Hinge: right valve with short strong anterior lateral; single central cardinal flanked by two deep triangular sockets; posterior lateral, short, stout; anterior and posterior laterals flanked on dorsal side by sockets. Left valve with two stout central cardinals separated by deep socket, anterior cardinal larger than posterior; anterior and posterior laterals short, formed from extension of valve margin, each flanked ventrally by deep socket.

$$\frac{RV \quad 01 \ 010 \ 10 \ \rightarrow}{LV \quad 10 \ 101 \ 01}$$

Anterior muscle scar elongate, narrow, kidney shaped. Posterior scar kidney shaped, slightly narrower than anterior scar. Pallial line entire. Internal valve margins smooth.

Dimensions

Holotype P142952	L 3.2	H 2.5
Paratype P142893	4.1	3.5
Paratype P142953	3 +	2.9 +
Paratype P142964	2.7	2.2

Type material. Holotype P142952, Paratype P142953, Paratype P142964, collected T. A. Darragh, 24 November 1992; Paratype P142893, collected T. A. Darragh, 17 February 1981.

Type locality. PL3003.

Occurrence and material. PL3001 (1 specimen); PL3003 (12 specimens).

Remarks. This species is characterised by the posterior section of the valve being larger than the anterior. The genus has a widespread distribution, occurring in North America from the Eocene and in Europe from the Miocene, but seems to have been recorded from the Paleocene only in New Zealand [*Myrtea microlirata* (Finlay & Marwick)]. *M. faseolata* has similar sculpture to *M. microlirata*, but is very much smaller, more elongate and the posterior section of the valve is relatively smaller. In addition the genus occurs from Late Oligocene to Early Pliocene in New Zealand. It is recorded from Late Pliocene to Recent in Australia.

Family THYASIRIDAE

Thyasira Leach, 1818

Type species. *Venus flexuosa* Montagu, 1803, Recent, Mediterranean.

Thyasira sp.

Fig. 4P–Q

Description. Shell thin, somewhat globose, subcircular, of average size for genus; umbo pointed, strongly prosogyral; lunule broad sunken. Anterior dorsal margin concave, anterior and ventral margins continuous, regularly convex; posterior dorsal and posterior margins convex continuous. Shallow sulcus running from umbo to posterior margin and forming notch in posterior margin. Ridge (submarginal sulcus) running from umbo parallel and close to posterior dorsal margin. Hinge plate edentulous. Sculpture of growth striae only.

Dimensions
Figured specimen P142949   L 7.2   H 7.2

Figured material. Figured specimen P142949, collected T. A. Darragh, 24 November 1992.

Occurrence and material. PL3003 (2 specimens).

Remarks. Both specimens are left valves. This taxon is very close to the type species of the genus in shape and hinge. It is somewhat similar to *Thyasira (Parathyasira) resupina* Iredale, Recent, New South Wales, but lacks the fine radial sculpture of that species. It is also somewhat similar to *T. (P.) notosulcata* Stilwell & Zinsmeister, late Eocene, Seymour Island. The genus is found in the Paleocene of Europe but is uncommon. It has not yet been reorded from the early Tertiary of the United States of America or New Zealand.

Kauffman (1969) suggested that fossil species of *Thyasira* had similar environmental requirements as the living species which have their greatest diversity in temperate waters and are not common in Arctic, Antarctic and tropical seas. He presented data that suggested that the present species would not be found with such a diversity of generic taxa as in the Pebble Point assemblage as a whole but some of the associated taxa would be found with it, e.g. *Propeamusium*, *Astarte* and *Cuspidaria*.

Family UNGULINIDAE

Felaniella (Zemysia) Finlay, 1926

Type species. *Lucina zelandica* Gray, 1835, Recent, New Zealand.

Felaniella (Zemysia) sp.

Fig. 4L–M

Description. Shell subquadrate, of average size for the genus (10×10 mm), almost equilateral; umbo scarcely projecting, orthogyral; anterior dorsal margin straight; anterior margin straight; ventral margin slightly convex; posterior margin slightly convex; posterior dorsal margin straight. No lunule or escutcheon. Sculpture of growth ridges only.

Hinge: left valve with long anterior lateral socket; stout central bifid cardinal, wide triangular socket posterior to it; posterior cardinal blade-like; long ligament groove.

Anterior muscle scar dorso-ventraly elongate, somewhat irregular, slightly larger than posterior scar; posterior scar slightly irregular in shape, dorso-ventraly elongate. Pallial line entire, deeply impressed. Internal margins of valve smooth.

Dimensions
Figured specimen P142897   L 1   H 1

Figured material. Figured specimen P142897, collected T. A. Darragh, 18 November 1984.

Material. PL3003 (two left valves).

Remarks. This has some resemblance to the type species, *Zemysia zelandica*, but the Pebble Point specimen is more quadrate, not so inflated and is higher than wide. It is close to *F. (Z.) elliptica* (Lamarck), Late Eocene, Paris Basin.

The subgenus has a wide distribution; the earliest records being in the Paleocene of Europe. In the southern hemisphere it is known from the Late Eocene and Miocene to Recent of New Zealand and the Recent of Australia. It has not been recorded as a fossil in Antarctica.

Family ERYCINIDAE

Borniola Iredale, 1924

Type species. *Bornia lepida* Hedley, 1906, Recent, New South Wales.

Borniola ? sp.

Fig. 4N–O

Description. Shell triangular, of average size for the genus; umbo pointed, slightly projecting, slightly prosogyral; valve strongly convex at flanks, central part of the disk flattened or slightly depressed; posterior dorsal margin straight, posterior and anterior margins short, strongly convex; ventral margin slightly concave.

Hinge with prominent socket posterior to long posterior tooth; central triangular resilifer; anterior tooth strong, projecting, hooked towards posterior at dorsal end, flanked on anterior by narrow socket. Muscle scars subequal, situated high in valve. Pallial line entire. Sculpture of growth lines only.

Dimensions
Figured specimen P142899   L 4.1   H 3.5

Figured material.   Figured specimen P142899, collected T. A. Darragh, 13 November 1984.

Occurrence and material.   PL3003 (one left valve).

Remarks.   The specimen resembles specimens of *Borniola reniformis* (Suter 1909), type species of the genus *Rochefortula* Finlay, 1927 (synonymised with *Borniola* by Ponder, 1967 but the reasons have not yet been published). The Pebble Point specimen is more trigonal, the resilium pit is much wider, the teeth diverge more, and the sockets are narrower. The genus is known from the Early Miocene to Recent of New Zealand and Recent of Australia. *Mysella trigonoelliptica* Stilwell & Zinsmeister, Late Eocene, Antarctica, may be a related taxon.

Family CYAMIIDAE

Cyamiocardium Soot-Ryen, 1951

Type species.   Cyamium denticulatum Smith, 1907, Recent, Antarctica.

Cyamiocardium silicula sp. nov.

Fig 4A–D, F

Description.   Shell roundly subquadrate, small (4–7 mm). Umbo broad, prosogyral, not projecting; posterior dorsal margin almost straight, merging rather abruptly with posterior margin; posterior margin gently curved merging imperceptibly with curved ventral margin; ventral margin merging imperceptibly with anterior margin; anterior dorsal margin straight, merging rapidly with curved anterior margin.

Sculpture of irregular growth striae and prominent growth interruptions. On unworn specimens very weak, low, broad radial ribs visible, ribs broader than interspaces.

Hinge: left valve with large, stout, bifid central cardinal, flanked by wide triangular sockets; sockets each flanked by blade-like teeth, posterior tooth much thinner and encroached upon by resilifer; wide resilifer between posterior tooth and valve margin. Right valve with two curved, strong blade-like cardinals, diverging from umbo,

separated by wide triangular socket and flanked by narrow deep sockets; posterior socket contiguous with resilifer on posterior side.

$$RV\ \underline{01010}\ \rightarrow$$
$$LV\ \ 10\wedge01$$

Anterior muscle scar D shaped, elongate, slightly smaller than posterior, both situated high in valve. Pallial line entire. Internal margin of valves weakly denticulate.

Dimensions
Holotype P142902	L 3.7	H 3.4
Paratype P142903	4.2	3.6
Paratype P142904	4.0	3.7

Type material.   Holotype P142902, collected T. A. Darragh, 27 November 1972; Paratypes P142903–5, collected T. A. Darragh, 13 November 1984.

Type locality.   PL3003.

Occurrence and material.   PL3001 (7 specimens), PL3003 (49 specimens), PL3004 (8 specimens).

Remarks.   Most specimens are worn, suggesting transport and few specimens show the external radial sculpture and the marginal denticulations. Specimens are fragmentary as they easily break at the prominent growth interruptions. Two specimens have countersunk gastropod boreholes.

The family is comprised mostly of genera occurring in the southern hemisphere and has a very poor fossil record. *Cyamiocardium* is known living from Antarctica, Chile and Australia. *C. denticulatum* (Smith) has a circum Antarctic distribution in depths from 5 to 1180 m. *C. silicula* is very similar to the latter, but is more quadrate and the radial sculpture is broader. It is not so equivalve as *C. dahli* Soot-Ryan and the umbo is directed more to the anterior. The sculpture seems similar to that of *C. dahli*.

Family ASTARTIDAE

Astarte (Astarte) J. Sowerby, 1816

Type species.   Venus scotica Maton & Rackett, 1807, Recent, Scotland.

Astarte (Astarte) notialis sp. nov.

Fig. 4H–K

Description.   Shell small (4–9), robust, trigonal to subquadrate. Umbos prosogyral, pointed. Posterior dorsal margin straight; posterior margin gently curved, merging imperceptibly into ventral margin; ventral margin gently convex; anterior margin strongly convex; anterior dorsal margin

straight or slightly concave. Escutchcon long, narrow, deep, sharply differentiated from valve surface. Lunule well developed, deep, lenticular, sharply differentiated from valve surface.

Hinge: left valve with anterior dorsal margin developed into an elongate lateral tooth; two thick cardinals separated by central triangular socket; elongate socket parallel to posterior dorsal margin. Right valve with clongate socket parallel to anterior dorsal margin; single strong, triangular central cardinal flanked by two deep triangular sockets and strong, elongate posterior lateral developed from posterior dorsal margin.

$$\text{RV} \quad \dfrac{1 \ n010 \ 0}{\ } \rightarrow$$
$$\text{LV} \quad \dfrac{\ }{0 \ n101 \ 1}$$

Adductor muscle scars deeply impressed, subequal; anterior D shaped; posterior muscle scar, slightly smaller than anterior, subcircular. Anterior pedal retractor scar immediately posterior to anterior adductor scar; dorsal pedal retractor scar beneath umbo in deep circular pit; posterior retractor scar contiguous with dorsal side of posterior adductor scar. Pallial line entire, deeply impressed. Internal margin of valves denticulate.

Sculpture close to umbo on some specimens of 9-10 sharp, commarginal ribs; on others rather coarse, wide ribs close to umbo; remainder of valve with widely spaced, very coarse growth rugae.

Dimensions

Holotype P142900	H 7.5	W 6.5	T 2.0
Paratype P142901	5.5	5.2	

Type material. Holotype P142900, collected T. A. Darragh, 8 March 1977; Paratype P142901, collected T. A. Darragh, 2 December 1985.

Type locality. PL3003.

Occurrence and material. PL3001 (25 specimens), PL3003 (267 specimens), PL3004 (27 specimens).

Remarks. On most specimens, particularly the larger, the fine sculpture near the umbo is abraded off. This is the most common bivalve in the fauna. Only two articulated pairs are known, all others are single valves. Many valves have gastropod boreholes.

Astarte notialis sp. nov. is similar to many species of *Astarte* from the Oligocene of Europe, such as *A. (A.) gracilis* Münster, which also have the cardinal teeth reduced in number. The European species all have regular sharp, well developed commarginal ribs unlike *A. notialis*.

Species of *Astarte* are not common in Paleocene strata. They occur in England, Denmark and Ukraine, but not in Belgium and France, and probably not in the Paleocene of North America. From Oligocene time on the genus is widespread in Europe through to Recent. It seems characteristic
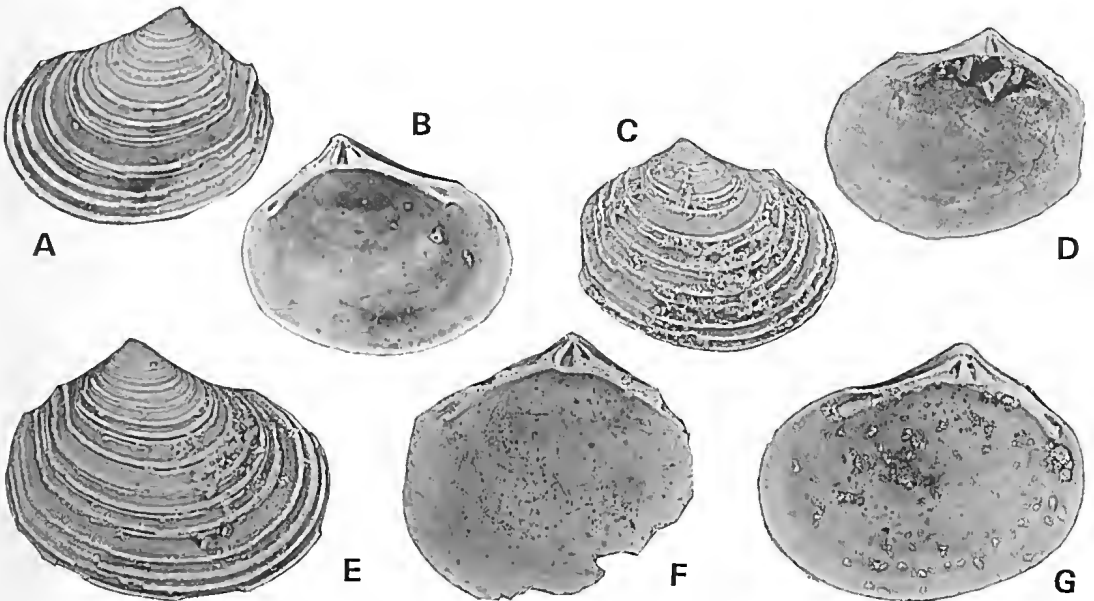
Fig. 5. A–G, *Myrtea faseolata* sp. nov. A–B, NMV P142964, paratype, PL3003, ×12.6. C–D, NMV P142893, paratype, PL3003, ×8. E, G, NMV P142952, holotype, PL3003, ×12.8. F, NMV P142953, paratype, PL3003, ×12.3.
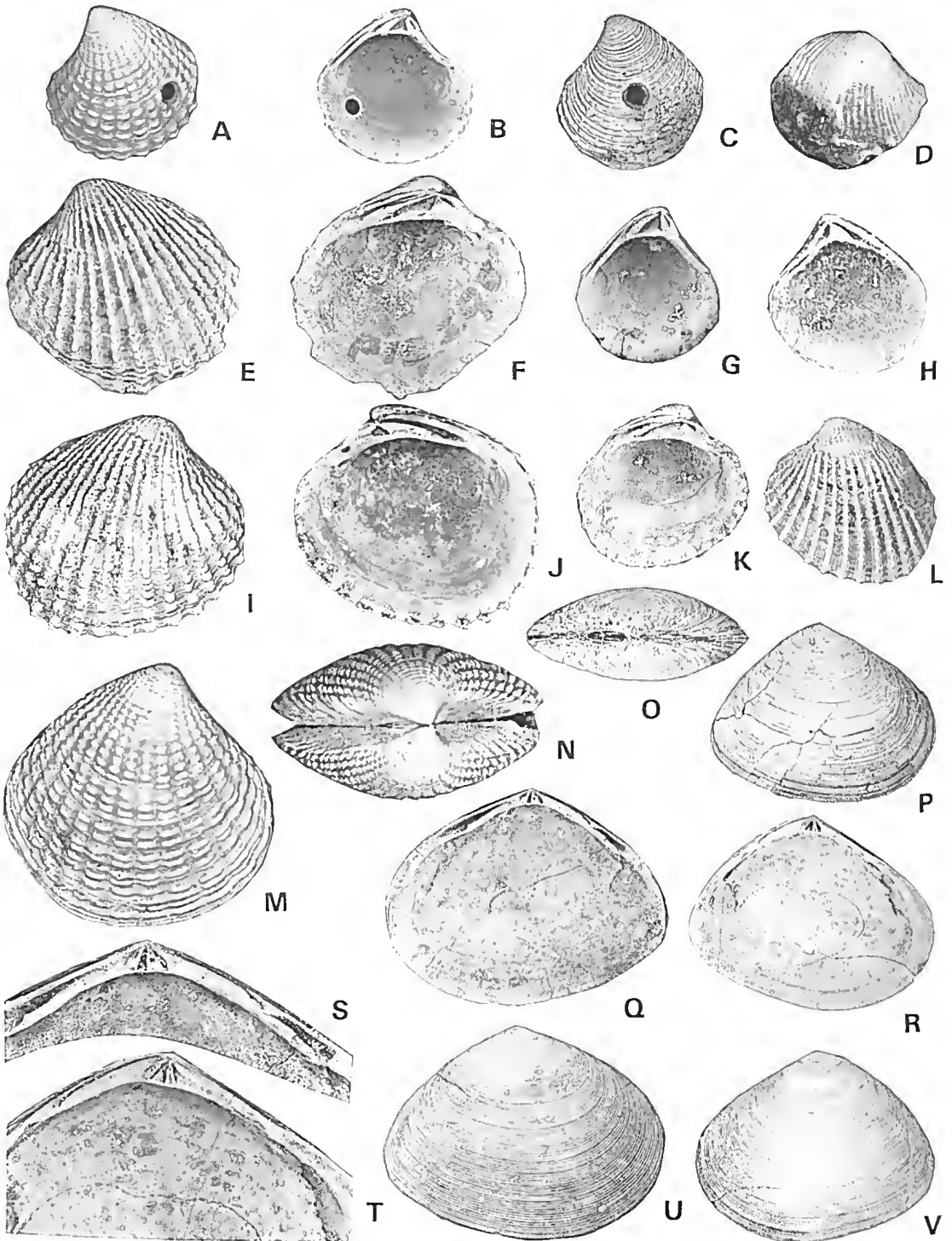
of cool water. The only other records of *Astarte* in the southern hemisphere are *Astarte longirostris* d'Orbigny and *A. antarctica* Thiele from waters surrounding the Antarctic, where they are abundant. The genus is not found in Australia above the Paleocene and it is not known from New Zealand or the Early Tertiary in Antarctica.

Family CARDITIDAE

Venericardia (Rotundicardia) Heaslip, 1968

Venericardia (Fasciculicardia) Maxwell 1969: 173.

Type species. *Venericardia rotunda* Lea, 1833, Eocene, south-eastern United States of America.

Early representatives of this group are common in the Tertiary of south-eastern Australia and New Zealand and received the name *Fasciculicardia* Maxwell, 1969 (type species, *Venericardia subintermedia* Suter 1917, Miocene, New Zealand). Maxwell (1992) pointed out that *Fasciculicardia* resembled the North American *Rotundicardia*, but that species of the former are more elongated anteroposteriorly and have a posterior truncation. On comparing specimens of *R. rotunda* with *F. latissima* (Tate), Late Eocene, Australia, the only differences seem to be shape, as the hinges are identical. The latter species tends to be not so rounded as the former, having a 'sharper' anterior end, but some specimens are as rounded as specimens of *rotunda*. For these reasons I prefer to use *Rotundicardia*, regarding *Fasciculicardia* as a synonym until a major revision of the New Zealand and Australian taxa provides firmer distinctions between them and the North American group.

The new species described here, *Venericardia (Rotundicardia) petraea* sp. nov. is more rounded than most of the younger species attributed to *Fasciculicardia* and in this respect is similar to species of *Rotundicardia*. The hinge seems to be identical to the latter.

The hinge of similarly sculptured members of the family in the Paris Basin seems to have a different arrangement of hinge teeth and they are probably not closely related to Australian and American species. The group is not known in the Antarctic.

Venericardia (Rotundicardia) petraea sp. nov.

Fig. 6E–F, 1–L

Description. Shell solid, equivalve, tumid, subreetangular; umbones searcely projecting, strongly prosogyral; anterior dorsal margin short, straight, posterior and ventral margins gently convex, anterior margin more strongly convex. Lunule small, well developed, heart shaped, sunken. Sculpture of 21 to 26 strong radial costae, narrower than interspaces, bearing prominent tubercles, in many specimens tubercles produced into prominent spines or scales. On some specimens costae flanked on either side by a weaker ridge.

Hinge in left valve, with long narrow posterior socket flanked ventrally by long blade-like posterior tooth; large triangular socket in front of it; small stout triangular almost peglike tooth under umbo directed vertically and immediately anterior to it a small socket.

Right valve hinge with small deep anterior socket and short weakly developed, bladclike tooth dorsal to it; narrow central triangular socket posterior to it; prominent central triangular tooth directed anteriorly with long narrow deep socket posterior to it, widening ventrally and flanked dorsally by a stout, long, narrow posterior tooth.

$$\text{RV } \underline{101010} \rightarrow$$
$$\text{LV } 010101$$

Anterior adductor muscle sear oval, elongate dorsoventraly. Posterior muscle sear subtriangular. Interior margin of valve strongly denticulate.

Dimensions

Holotype P142906	L 10	W 9	T 3.5
Paratype P142907	11	11	4
Paratype P142908	9.5	9	3.5

Type material. Holotype P142906, collected T. A. Darragh, 17 February 1981; Paratype P142907, collected T. A. Darragh, 8 May 1979; Paratype P142908, collected T. A. Darragh, 19 November 1970.

Type locality. PL3003.

Occurrence and material. PL3001 (25 specimens), PL3003 (54 specimens), PL3004 (3 specimens).

Remarks. Only one specimen is an articulated

Fig. 6. A–C, G–H, M–N, *Carditellopsis bellissima* sp. nov. A–B, NMV P142911, paratype, PL3003, showing gastropod borehole, ×7.75. C, NMV P142968, paratype, PL3003, showing gastropod borehole, ×6. G, NMV P142969, paratype, PL3003, ×6. H, NMV P142915, paratype, PL3003, ×6. M–N, NMV P1142910, holotype, PL3003, ×8. D, *Verticordia* sp. NMV P142950, PL3004, ×3.5. E–F, 1–L, *Venericardia (Rotundicardia) petraea* sp. nov. E–F, NMV P142908, paratype, PL3004, ×3.5. 1–J, NMV P142906, holotype, PL3003, ×3.6. K–L, NMV P142907, paratype, PL3003, ×2.6. O–V, *Bertinella lapidaria* sp. nov. O–P, NMV P142922, paratype, PL3003, ×1.7. Q, U, NMV P142920, paratype, PL3004, ×1.7. S, NMV P142920, paratype, ×3.4. R, V, NMV P142921, holotype, PL3003, ×1.8. T, NMV P142921, holotype, ×3.4.

pair. This species is closely related to *Venericardia (Rotundicardia) latissima* (Tate), Late Eocene of southern Australia, from which it differs by having the triangular right valve central tooth oriented obliquely rather than laterally as in *V. (R.) latissima*, the outline is more rounded with a broader anterior end and it has fewer ribs (21–26 rather than 25–29) than *V. (R.) latissima*.

Carditellopsis Iredale, 1936

Type species. *Carditella elegantula* Tate & May, 1901, Recent, Tasmania.

Carditellopsis bellissima sp. nov.

Fig. 6A–C, G–H, M–N

Description. Shell small, of average size for genus (2.9×3.0–4.6×4.7 mm), roundly trigonal, slightly higher than wide, equivalve, with prominent umbos, curved anteriorly; anterior dorsal margin concave, anterior, ventral and posterior margins convex, merging imperceptibly, posterior dorsal margin straight. Lunule heart shaped, smooth, well differentiated. Escutcheon long, narrow, smooth, bounded by sharp ridge. Sculpture of about 15 thick, commarginal, erect lamellae, continuous on dorsal half of valve, broken by radial incisions on ventral posterior half of valve. On some specimens, commarginal sculpture broken up into a series of aligned coarse elongate tubercles over entire surface of valve.

Hinge: left valve, posterior socket long, flanked by slight ridge or swelling on inner side of hinge and edge of valve; posterior cardinal strong, long and narrowing anteriorly; large central triangular socket and short strong, almost peg-like anterior cardinal; anterior lateral marginal, formed from raised surface of edge of valve, a little distant from anterior cardinal. Right valve anterior socket long, deep, flanked by ridge on interior side of hinge and thin edge of valve; central cardinal triangular, strong, slightly bifid; posterior marginal lateral well developed, formed by raised extension of valve margin. Ligament external.

$$\begin{array}{ll} \text{RV} & \dfrac{1 \quad - 010 - (1)0(1)}{(1)0(1) - 101 - \quad 1} \rightarrow \\ \text{LV} & \end{array}$$

Anterior muscle scar kidney shaped, longer than wide; posterior scar subtriangular. Pallial line entire. Internal ventral margin with about 16 coarse denticulations.

Dimensions

Holotype P142910	W 4.6	H 4.7	T 2.8
Paratype P142911	2.9	3.0	
Paratype P142968	3.6	3.8	
Paratype P142969	3.5	3.8	
Paratype P142915	3.8	3.9	

Type material. Holotype P142910, collected T. A. Darragh, 17 February 1981; Paratype P142911, collected T. A. Darragh, 2 December 1984; Paratype P142968-9, collected T. A. Darragh, 24 November 1992; Paratype P142915, collected T. A. Darragh, 8 March 1971.

Type locality. PL3003.

Occurrence and material. PL3001 (1 specimen), PL3003 (45 specimens), PL3004 (5 specimens).

Remarks. There are two articulated pairs present in the sample. Three specimens have countersunk gastropod boreholes. The pair of posterior laterals in the left valve, stated by some authors to be present in this group, is barely recognisable in this species. The hinge is similar to that of *Carditellopsis elegantula* (= *valida* Vereo), Recent, southern Australia, but the teeth in the latter are slightly curved to the anterior because the umbo and hinge area are slightly curved. The sculpture of *C. bellissima* sp. nov. is much coarser than that of the *C. elegantula* and the valves are not so tumid. *C. bellissima* sp. nov. is probably ancestral to *C. rugosa* (Tate) from the Late Eocene of southern Australia, but the sculpture is much coarser than that present on the latter.

The ancestral genus seems to be *Vetericardia* of the Late Cretaceous of North America, which has similar sculpture and hinge to *Carditellopsis*. Somewhat similar species in the early Tertiary of Europe were referred to *Choniocardia* by Glibert & Van de Poel (1970).

The group seems to be absent from the early Tertiary of New Zealand and Antarctica.

Family LAHILLIIDAE

Lahillia Cossmann, 1899

Lahilleona Finlay & Marwick 1937: 31.

Type species. *Amathusia angulata* Philippi, 1887, Miocene, Chile.

Zinsmeister (1984) showed that species of *Lahillia* possessed a pallial sinus and synonymised *Lahilleona* with *Lahillia* since the feature alleged to separate them was the absence of a sinus in the latter and its presence in *Lahilleona*.

Lahillia australica Singleton, 1943

Fig. 7A–G

Lahillia australica Singleton 1943: 273, pl. 12, figs 3–5.— Ludbrook 1973: pl. 24, figs 4–5.

Description. Shell large (67×64–80×70), thick, inequivalve, almost equilateral, moderately inflated, ovate to subtrigonal; anterior and posterior dorsal margins concave; posterior dorsal margin merging into posterior margin; posterior margin slightly convex; ventral and anterior margins convex, continuous, abruptly truncated by anterior dorsal margin. Umbones slightly prosogyral, projecting, subcentral. Posterior ridge on valve ill-defined. Lunule large, lanceolate, sunken, poorly defined. Surface of valve sculptured with irregularly spaced growth striae only.

Hinge plate thick. Left valve with stout peg-like, subcentral cardinal tooth flanked with deep sockets; posterior cardinal thin, poorly defined; nymph large, flattened, produced dorsally beyond hinge plate, separated from posterior dorsal ramp by deep ligamental groove; posterior lateral short, stout, flanked dorsally by long narrow socket; small triangular area at umbo against posterior cardinal forming pseudo resilifer. Right valve with anterior cardinal tooth weak, poorly defined; posterior cardinal prominent, stout peg-like, separated from anterior cardinal by deep triangular socket; nymph broad triangular extended; posterior lateral short stout, flanked dorsally by deep, wide socket.

$$RV \ \underline{01 \ n \ 101} \rightarrow$$
$$LV \ \ 1 \ \ \ n1010$$

Pallial line faint with shallow sinus. Internal valve margin smooth.

Dimensions

Holotype P128034	L 77	W 73	T 26
Paratype P128036	78	72	28
Paratype P128035	77	71	25
Figured specimen P142917	80	71	25
Figured specimen P142916	75	69	25

Types. Holotype P128034 (MUGD 1865), collected G. Baker, January 1942; Paratypes P128035–6 (MUGD 1866–7), collected W. J. Parr, October 1915, presented December 1943. Figured specimens P142916–7, collected T. A. Darragh, 8 May 1979.

Type locality. Coastal cliffs 2½ miles southeast of Princetown, Victoria, second point north-west of Pebble Point (PL 3004, Buckley Point).

Occurrence and material. PL3001 (5 specimens), PL3003 (26 specimens), PL3004 (11 specimens), PL3005 (11 specimens).

Remarks. This species is more common than would be supposed from the above numbers, which are low owing to the difficulty of collecting reasonably complete specimens.

Species of the genus are distributed from the Late Cretaceous to Early Miocene in New Zealand (Late Cretaceous–Early Paleocene), New Caledonia (Late Cretaceous), southern South America (Late Cretaceous–Early Miocene) and Antarctica (Late Cretaceous–Late Eocene). Shells are devoid of sculpture and all species look very similar, differing in shape. Compared with *L. neozelanica* (Marshall & Murdoch) the umbones of *L. australica* are more slightly orthogyral and not so produced, the outline is oval rather than subtriangular, the lunule is much less developed and the right anterior lateral is much stronger than in *L. neozelanica* (it is virtually obsolete in the latter). Compared with *L. larsoni* (Sharman & Newton) (Late Cretaceous and Early Paleocene, Antarctica), *L. australica* is more equilateral and not so elongate, the umbones are not so prosogyral and it has a more pointed anterior end. *L. huberi* Zinsmeister (early Paleocene, Antarctica) is very close to *L. australica* but the latter has higher umbones. *L. huisi* (Wilekens) (Late Cretaceous, Patagonia) is somewhat similar in shape, but *L. australica* is relatively higher and narrower. Of all the described early Tertiary species, the one that seems closest to *L. australica* is *L. wilckensi* Zinsmeister (Late Eocene, Antarctica) but that species is slightly more elongate than the former.

Freneix (1958) described *Lahillia (Lahilleona) marwicki* from the Late Cretaceous of New Caledonia based on two internal moulds which did not show the hinge. It is not clear from the figures if this determination is correct, however Freneix (1980) described and illustrated an internal mould showing a shallow pallial sinus and hinge of the left valve which confirms the record of the genus.

Family TELLINIDAE

Bertinella Glibert & Van de Poel, 1967

Type species. Tellina donacialis Lamarck, 1806, Eocene, Paris Basin.

Bertinella lapidaria sp. nov.

Fig. 6O–V

Description. Shell subtrigonal, equivalve, of average size (17×12–22×17); umbones sharp, not projecting; anterior dorsal margin straight; anterior margin strongly rounded, merging imperceptibly with ventral margin; ventral margin gently rounded; posterior dorsal margin straight, merging at sharp angle with ventral margin to form sharp
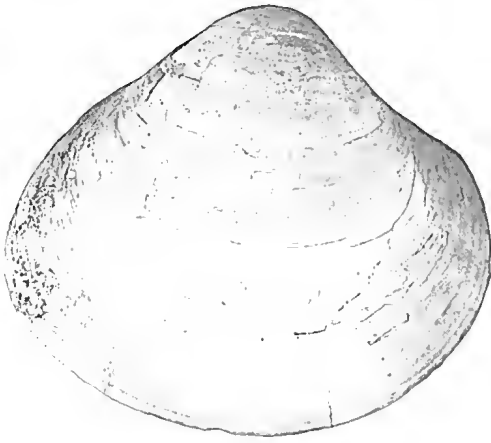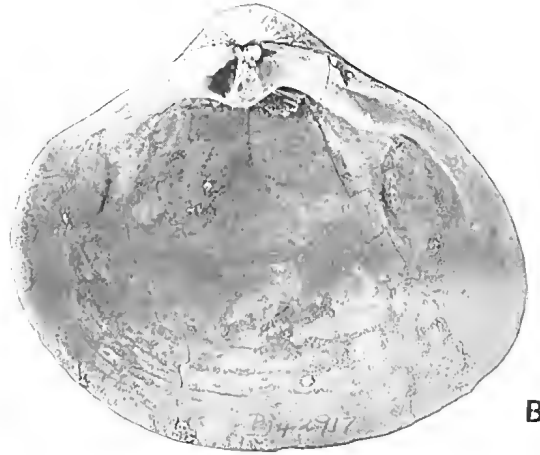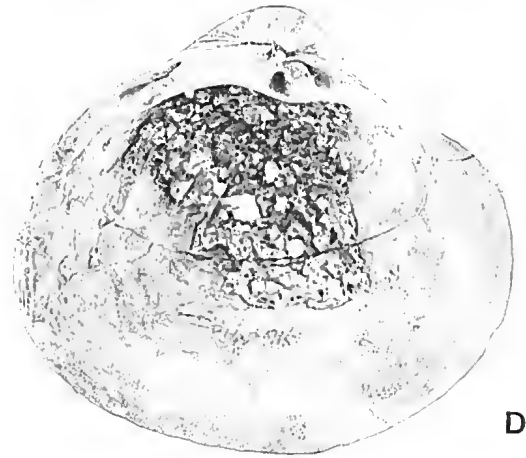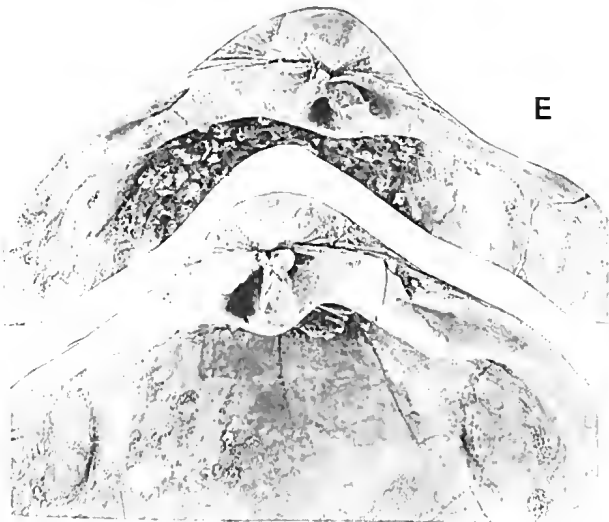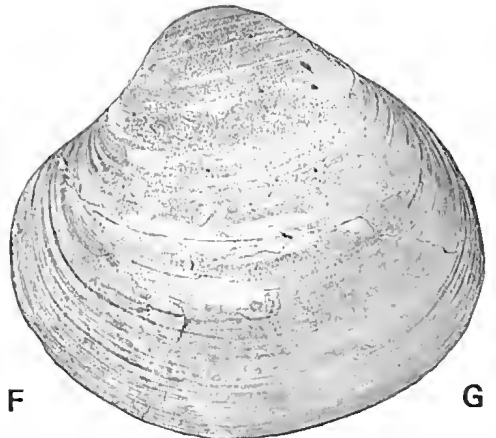
point. Siphonal ridge present running from umbo to posterior point. Right valve with slight flexure on posterior third of flank. Eseuteheon very narrow, well defined; lunule narrow and weak.

Seulpture of thin, elosely spaced, commarginal, rounded riblets, slightly narrower than interspaces. No trace of radial sculpture.

Hinge: left valve with weak posterior lateral formed by margin of valve; posterior cardinal blade-like, flanked anteriorly by triangular soeket; anterior eardinal narrow, triangular, bifid, flanked anteriorly by wide triangular soeket; anterior lateral weak formed by valve margin. Right valve with large anterior socket between anterior dorsal margin and short pointed, blade-like anterior lateral; anterior eardinal broad based and beeoming blade-like at top; wide, triangular socket posterior to it; strong triangular bifid cardinal posterior to socket; posterior lateral short, pointed, blade-like; long deep socket between it and valve margin.

$$\begin{array}{llll} RV & \underline{01} & \underline{0 \wedge 01} & \underline{10} \rightarrow \\ LV & 1\ 1 & 10 \wedge 0 & 1 \end{array}$$

Anterior muscle scar elongate, D shaped, higher than wide; posterior musele scar subeircular. Pallial line with large rounded pallial sinus extending to eentre of valve. Internal valve margins smooth.

Dimensions

Holotype P142921	L 21	H 16.5	T 4.5
Paratype P142922	19.5	16	8.5 (pair)
Paratype P142920	24	19	4

Type material. Holotype P142921, Paratype P142922 collected T. A. Darragh, 17 February 1981; Paratype P142920, collected T. A. Darragh, 19 November 1970.

Type locality. PL3003.

Occurrence and material. PL3001 (40 specimens), PL3003 (70 specimens), PL3004 (4 specimens), PL3176 (3 specimens), PL3177 (1 specimen).

Remarks. Complete well preserved specimens of this speeies, though thin and fragile, are quite common and the sample eontains eight pairs. This suggests the specimens may not have been subject to as much transport as other species. Two specimens have gastropod boreholes.

The correet genus to which this species should be assigned is uncerlain beeause of the large number of taxa available in this family. For the present I have included it, with some diffidenee, in *Bertinella*, beeause of its similarity to other species

assigned to that genus which occur in the Paleocene to Oligocene of Europe and Ukraine. The type speeies, *Bertinella donaciformis* (Lamarek), is smooth and lacks an eseutchcon, but other species included in the genus by Glibert & Van der Poel (1967), such *B. elegans* (Dcshayes) and *B. beyrichi* (Deshayes), have an eseuteheon and eommarginal ribs and are similar to *B. lapidaria* sp. nov. *Tellina dimidiata* v. Koenen, Early Oligocene, Germany seems to be anothcr member of this group and is also very similar to the latter. *Tellina williamsi* Clark, Paleocene to Eoeene of the eastern United States of America may be a representative of this group.

Bertinella is elose to *Serratina*, type species *Tellina serrata* Broechi, from the late Tertiary and Recent of Europe and may possibly be a synonym. Because *S. serrata* has a very prominent escutcheon and a posterior fold running from umbo to the postero-ventral angle on the right valve and a eorresponding groove on the left valve, whieh are lacking in *B. lapidaria*, 1 have used *Bertinella*.

Family VENERIDAE

Dosinia (Dosinobia) Finlay & Marwick, 1937

Type species. Dosinia (Kereia) ongleyi Marwick, 1927, Paleocene, New Zealand.

Dosinia (Dosinobia) saxatilis sp. nov.

Fig. 8P–V

Description. Shell small to medium size for the genus (16×15–18×16), subeircular, slightly inflated, posterior end slightly truneated. Lunule well defined by incised line; escutcheon well defined. Sculpture of thin, close spaeed, eommarginal lamellae.

Hinge: left valve with long groove between margin of valve and anterior cardinal and lateral; anterior cardinal blade-like, strong, eurved, extending anteriorly as a low ridge and produced into a short blade-like anterior lateral; anterior cardinal flanked posteriorly by long curved, narrow triangular socket; central cardinal tooth strong, narrow, triangular, flanked posteriorly by wide triangular soeket; posterior eardinal tooth long, thin. Right valve with shallow round socket anteriorly continuous with socket between anterior cardinals, dorsal to it a thin, well developed anterior cardinal tooth flanked posteriorly by deep narrow

---

Fig. 7. A–G, *Lahillia australica* Singleton. A–B, NMV P142917, PL3003, ×0.8. C, NMV P128034, holotype, second point NW of Pebble Point, ×0.8, D, G, NMV P142916, PL3003, ×0.8. E, NMV P142916, ×1.1. F, NMV P142917, ×1.1.
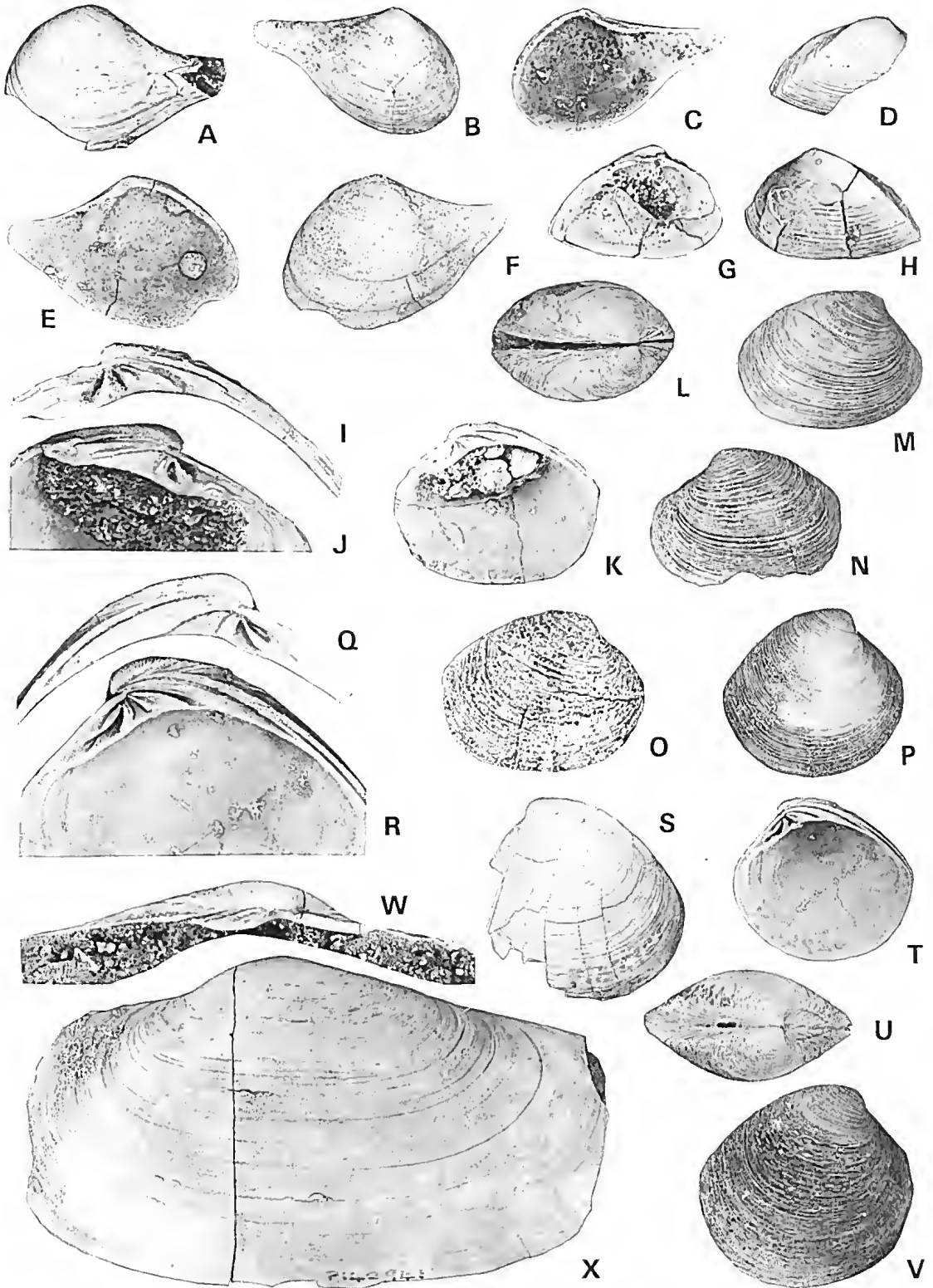
socket; strong, very narrow, triangular grooved cardinal posterior to socket; deep triangular central socket; posterior cardinal tooth strong, triangular, bifid, elongate, flanked posteriorly by deep narrow socket.

RV $\underline{0 \wedge 0101 \ 0} \to$
LV 101010 1

Pallial sinus pointed, wide and deep, extending a third of the distance towards the posterior. Internal margins of valves smooth.

Dimensions

Holotype P142926	L 16	H 15	T 4.5
Paratype P142924	19	19	10 pair
Paratype P142927	—	20	7

Type material. Holotype P142926 collected 8 March 1971, Paratype P142924 collected T. A. Darragh, 23 November 1992, Paratype P142927 collected T. A. Darragh, 17 February 1981.

Type locality. PL3003.

Occurrence and material. PL3001 (13 specimens), PL3003 (43 specimens), PL3004 (9 specimens), PL3005 (1 specimen), PL3176 (2 specimens), PL3177 (1 specimen).

Remarks. Only two specimens are articulated pairs. This is one of the earliest known members of the subfamily Dosiniinae. The hinge of this species is close to that described for *Dosinia (Dosinobia) ongleyi*, Early Paleocene, New Zealand, but the anterior lateral is a little shorter, the right posterior cardinal is wider and the right central cardinal narrower than in the latter. *Dosinia (Dosinobia) saxatilis* sp. nov. is much more convex than either *D. (D.) ongleyi* or *D. (D.) perplexa* Marwick, Paleocene, New Zealand, but the sculpture is very similar, though more lamellose in *D. (D) saxatilis*. The escutcheon is much wider than that in *D. ongleyi.*

Finlay & Marwick (1937) in discussing the distribution of *Dosinia* and its allies pointed out that the earliest Tertiary records of the group are in New Zealand. The occurrence in Australia of this new species of the genus suggests that the group may have had a southern hemisphere origin. There is nothing similar in the Antarctic and there are no known records of *Dosinobia* above the Paleocene

in Australia. Freneix (1958) recorded *Dosinobia* sp. cf. *D. perplexa* from the Late Cretaceous of New Caledonia. The material consisted of internal moulds and the determination seems doubtful.

Callistina (Tikia) Marwick, 1926

Type species. *Callista thomsoni* Woods, 1917, Late Cretaceous, New Zealand.

Callistina (Tikia) ? scopulensis sp. nov.

Fig. 8I–O

Description. Shell of medium size (14×10–19×15), elongate-ovate, almost subrectangular, tumid; posterior dorsal margin gently convex, abruptly truncated by posterior margin; ventral margin slightly convex; anterior margin strongly convex; anterior dorsal margin short, straight. Umbos strongly prosogyral, not projecting. Lunule not sunken, bounded by groove; escutcheon well developed, elongate-lanceolate. Sculpture of thin erect, somewhat irregularly spaced commarginal lamellae; no radial elements present. Interior of valve margins smooth. Pallial sinus not visible.

Hinge: left valve with posterior cardinal long, blade-like; wide triangular socket anterior to it, socket bounded on anterior by thin curved blade-like central cardinal tooth, separated from anterior cardinal by deep triangular socket; anterior cardinal strong, high, blade-like, curved; anterior lateral short, strong, blade-like. Right valve with shallow anterior socket, anterior and ventral to anterior cardinal; anterior cardinal weak, curved, separated from central cardinal by deep narrow socket; central cardinal stout, subtriangular, separated from posterior cardinal by deep triangular socket; posterior cardinal large, strongly bifid, triangular, directed anteriorly, flanked posteriorly by long narrow socket. Ligament external.

RV $\underline{0 \wedge 0101 \ 0} \to$
LV 101010 1

Dimensions

Holotype P142929	L 16	H 13	T 9
Paratype P142930	18	15	10

Fig. 8. A–C, E–F, *Cuspidaria* sp. A, NMV P142948, PL3001, ×3.3. B–C, NMV P142951, PL3003, ×3.6. E–F, NMV P142946, PL3004, ×3.6. D, G–H, *Caryocorbula* sp. NMV P142939, pair, PL3003, ×3.6. I–O, *Callistina (Tikia)? scopulensis* sp. nov. I, NMV P142930, paratype, PL3001, ×3.5. J, NMV P142931, paratype, PL3001, ×3.6. K, O, NMV P142930, paratype, PL3001, ×1.7. L–M, NMV P142929, holotype, PL3004, ×1.75. N, NMV P142931, paratype, PL3001, ×1.7. P–V, *Dosinia (Dosinobia) saxatilis* sp. nov. P, T, NMV P142926, holotype, PL3003, ×1.75. Q, NMV P142927, paratype, PL3003, ×3.7. R, NMV P142926, holotype, ×3.7. S, NMV P142927, paratype, PL3003, ×1.8. U–V, NMV P142924, paratype, PL3004, ×1.7. W–X, *Panopea* sp. W, NMV P142941, between Rivernook and Pebble Point, ×1.7. X, P142941, ×1.5.

Type material. Holotype P142929 collected T. A. Darragh, 19 November 1970, Paratypes P142930–1 collected T. A. Darragh, 28 February 1970.

Type locality. PL3004.

Occurrence and material. PL3001 (6 specimens), PL3003 (8 specimens), PL3004 (1 specimen).

Remarks. Three of the specimens are articulated pairs. This species is provisionally placed in *Callistina (Tikia)* because the hinge is somewhat similar and both *Callistina* and *Tikia* have a smooth internal valve margin, and possess an escutcheon and a simple triangular pallial sinus. *Callistina (Tikia)? scopulensis* sp. nov. is more rectangular than most species in these taxa and has a sculpture of commarginal raised lamellae rather than grooves or ridges. *Callistina* was synonymised with *Aphrodina* in the 'Treatise' but *Aphrodina* has no escutcheon. *Tikia* has been recorded from the Late Cretaceous of New Zealand, New Caledonia and Antarctica. There seems to be nothing quite like this species in the Tertiary of of any of these countries.

Family CORBULIDAE

Caryocorbula Gardner, 1926

Type species. *Corbula alabamiensis* Lea, 1833, Eocene, United States of America.

Caryocorbula sp.

Fig. 8D, G–H

Description. Shell small (7.5 × 5), solid, triangular, slightly inequilateral. Umbo orthogyral, situated slightly anterior to mid-line. Anterior and anterior dorsal margins not separated, convex; ventral margin slightly convex; posterior dorsal and posterior margins merging imperceptibly, slightly convex, abruptly truncated at ventral margin to form sharp point. Posterior area narrow, bounded by sharp ridge running from umbo to posterior point. Sculpture of rounded commarginal costae, about as wide as interspaces, less well developed on posterior area.

Hinge: left valve damaged. Right valve with prominent peglike tooth anterior to resilifer. Pallial line well marked; pallial sinus merely a slight indentation.

Dimensions
Figured specimen P142939   L 7.5   H 5

Figured material. Figured specimen P142939, collected T. A. Darragh, 17 February 1981.

Occurrence and material. PL3003 (6 specimens).

Remarks. One specimen is a well preserved fragmentary articulated pair and the others are very worn. This species has some resemblance to *Caryocorbula waihaoensis* Finlay & Marwick, Middle Eocene?, New Zealand, but the latter is more quadrate and not so triangular. It is very similar in shape and sculpture to *C. parilis* (Gabb), Middle Eocene, California.

The genus has a cosmopolitan distribution and is known from the Early Eocene of New Zealand, the Paleocene of California, south-eastern United States of America, India, Belgium, and Ukraine. There are no comparable species in the early Tertiary of the Antarctic and South America.

This species bears a superficial resemblance to *Corbula pyxidata* Tate, Late Eocene, southern Australia, but has not so large a posterior area, is not so inflated and lacks any suggestion of a posterior rostrum. Some specimens of *C. pyxidata* have accessory plates preserved and all specimens are rostrate, features that suggest it belongs in *Caestocorbula*.

Family HIATELLIDAE

Panopea Menard, 1807

Type species. *Mya glycymeris* Born, 1778, Recent, Mediterranean.

Panopea sp.

Fig. 8W–X

Description. Shell, relatively solid, elongate oval, of medium size for genus (60–75 mm), regularly convex, tapering very slightly posteriorly, only slight gape. Umbo broad, strongly incurved, orthogyral, situated at about anterior $\frac{1}{3}$ third of shell length. Anterior dorsal margin short, straight and subparallel with ventral margin; posterior dorsal margin slightly concave; anterior margin strongly convex, merging imperceptibly into ventral margin; ventral margin very gently convex; posterior margin strongly convex.

Sculpture of low coarse, commarginal folds extending about 5 mm from umbo, fading rapidly ventrally. Major portion of valve sculptured with growth striae only; flank covered with microscopic sculpture of fine radial, nodulose threadlets, eroded off most specimens.

Hinge of left valve with prominent elongate triangular resilifer, with deep incision close to valve edge and single blade-like tooth. Right valve not known.

Pallial sinus extending to beneath umbo.

Dimensions
Figured specimen P142941   L 60+   H 35

Figured material. Figured specimen P142941, J. Dennant Collection.

Occurrence and material. PL3001 (1 specimen), PL3003 (3 specimens), PL3005 (4 specimens); between Rivernook and Pebble Point (1 specimen).

Remarks. All specimens are fragmentary. Of Australian species the Pebble Point taxon comes closest to *Panopea agnewi* (Tenison Woods), Early Miocene, but the umbo is broader and not so far forward, and the valve surface has coarse folds only near the umbo unlike *P. agnewi* in which the folds extend well down the valve. *P. ralphi* Finlay, Middle Miocene, has the umbo situated even further forward than *P. angnewi*. The Pebble Point taxon is distinguished from species from the later Tertiary of Victoria by its relatively smooth surface, lacking folds, and its small gape.

This species has some resemblance to the smooth forms of *Panopea gurgitis* (var. *neocomiensis*), Cretaceous, Europe, but that species has the umbo situated further towards the anterior. It is very similar to *P. eightsi* Stilwell & Zinsmeister, Late Eocene, La Meseta Formation, Seymour Island and also to *P. elongata* Conrad, Paleocene, Acquia Formation, eastern U.S.A.

Cuspidaria Nardo, 1840

Type species. *Tellina cuspidata* Olivi, 1792, Recent, Mediterranean.

Family CUSPIDARIIDAE

Cuspidaria sp.

Fig. 8A–C, E–F

Description. Shell elongate ovate, rostrate, tumid, of average size for genus (10×6.5 mm); umbo opisthogyral, not projecting; anterior dorsal margin long convex; anterior margin short, strongly convex, continuous with dorsal margin; ventral margin convex then concave where it forms posterior rostrum; posterior dorsal margin concave extending to form posterior rostrum. Sculpture of thin, widely spaced, commarginal ribs present either on dorsal third of valve only or over whole of valve, other portion of valve sculptured with prominent growth ridges. Rostrum with three fine widely spaced radial threads, one of which bounds rostrum ventrally. Hinge with small resilifer under umbo, teeth if present in left valve not visible on available material. Right valve with long posterior lateral tooth. Posterior adductor scar subtriangular deeply sunken; anterior scar not visible.

Dimensions

Figured specimen P142946	L 10	H 6.5
Figured specimen P142948	9.5	7
Figured specimen P142951	8	5.5

Figured material. Figured specimens P142946, P142948, P142950 collected T. A. Darragh, 23 November 1992.

Occurrence and material. PL3001 (1 specimen), PL3003 (2 specimens), PL3004 (1 specimen).

Remarks. Three specimens are left valves and are incomplete or worn. The right valve is complete and relatively unworn. This taxon is very close in morphology to *Cuspidaria subrostrata* Tate, Middle Miocene, Victoria. The sculpture is similar but the outline is subcircular rather than elliptical. In shape it resembles *Cuspidaria raincourti* Cossmann, Eocene, Paris Basin, but that species has close-set, fine commarginal ribs covering the whole valve. The genus occurs rarely in the Paleocene of Europe but is not recorded from the Early Tertiary of New Zealand, Antarctica or from the Paleocene of the United States.

Family VERTICORDIIDAE

Verticordia Sowerby, 1844

Type species. *Hippagus ? cardiiformis* Sowerby, 1844, Pliocene, England.

Verticordia sp.

Fig. 6D

Description. Shell small, of average size for genus, subrectangular; umbo prosogyral; sculptured with about 29 well spaced ribs. Valve surface covered with fine granulation.

Dimensions
Figured specimen P142950   L 6+   H 5.5+

Figured material. Figured specimen P142950, collected T. A. Darragh, 23 November 1992.

Occurrence and material. PL3003 (3 fragments), PL3004 (1 specimen).

Remarks. All specimens are fragmentary, but one fragment shows well preserved sculpture.

The genus occurs in the Paleocene and Eocene of Europe and the Paleocene of North America. The material is not well enough preserved for detailed comparison, but the available material bears a close resemblance to *Verticordia granulosa* Ravn, Early Paleocene, Denmark and Ukraine.

ACKNOWLEDGEMENTS

REFERENCES

ADEGOKE, O. S., 1977. Stratigraphy and Paleontology of the Ewekoro Formation (Palcocene) of south-western Nigeria. *Bulletins of American Paleontology* 295: 379 p., 50 pls.

ANDERSON, H.-J., 1973. Die Fauna der paläocänen hückclhovencr Schichten aus dcm Schacht Sophia Jacoba 6 (Erkelenzer Horst, Niederrheinische Bucht) Teil 1, Bivalvia. Palaeotaxodonta und Pteriomorpha. *Geologica et Palaeontologica* 7: 175–187, 3 pls.

ANDERSON, H.-J., 1974. Die Fauna der paläocänen hückelhovener Schichten aus dem Schacht Sophia Jacoba 6 (Erkelenzcr Horst, Nicderrheinische Bucht) Teil 2, Bivalvia. Hetcrodonta und Anomalodesmata. *Geologica et Palaeontologica* 8: 159–192, 7 pls.

BAKER, G., 1943. Eoccne dcposits south-east of Princetown, Victoria. *Proceedings of the Royal Society of Victoria* 55: 237–254, pl. 10.

BAKER, G., 1950. Gcology and physiography of the Moonlight Head district, Victoria. *Proceedings of the Royal Society of Victoria* 60: 17–43, pls 1–4.

BEU, A. G. & MAXWELL, P. A., 1990. Cenozoic Mollusca of New Zealand. *New Zealand Geological Survey Paleontological Bulletin* 58: 518 p., 57 pls.

BOYD, D. W. & NEWELL, N. D., 1969. Limitations of Bernard and Municr–Chalmas System for bivalve hinge notation. In *Treatise on Invertebrate Paleontology*, C. Teichert, cd., N Mollusca 6, vol. 2: N908–913.

DARRAGH, T. A., 1985. Molluscan biogeography and biostratigraphy of the Tertiary of southeastern Australia. *Alchcringa* 9(1–2): 83–109, figs 1–9.

DARRAGH, T. A., 1986. The Cainozoic Trigoniidac of Australia. *Alchcringa* 10(1): 1–34, figs 1–11.

DARRAGH, T. A. & KENDRICK, G. W., 1991. Maastrichtian Bivalvia (excluding Inoccramidae) from the Miria Formation, Carnarvon Basin, north Western Australia. *Records of the Western Australian Museum Supplement* 36: 102, 26 figs.

DARRAGH, T. A. & KENDRICK, G. W., 1994. Maastrichtian Scaphopoda and Gastropoda from the Miria Formation, Carnarvon Basin, north Westcrn Australia. *Records of the Western Australian Museum Supplement* 48: 76, 14 figs.

DAVIES, A. M., 1929. Faunal migrations since the Cretaccous Pcriod. *Proceedings of the Geological Association* 40: 307–327.

DAVIES, A. M., 1934. *Tertiary Faunas* vol. 2, Thomas Murby & Co., London.

EKMAN, S., 1967. *Zoogeography of the Sea.* Sidgwick & Jackson, London.

FINLAY, H. J. & MARWICK, J., 1937. The Wangaloan and associated molluscan faunas of Kaitangata–Green Island Subdivision. *Geological Survey of New Zealand Palaeontological Bulletin* 15: 140 p., 17 pls.

FRAKES, L. A. *et. al.*, 1987. Australian Cretaceous shorelines, stage by stage. *Palaeogeography, Palaeoclimatology, Palaeoecology* 59: 31–48, 13 figs.

FRENEIX, S., 1958. Contribution à l'étude des Lamellibranches du Crétacé de Nouvcllc-Calédonie. *Sciences de la Terre* 4(3–4): 153–207, 3 pls.

FRENEIX, S., 1980. Bivalves Néocrétacés dc Nouvellc-Caledonie signification biogéographique, biostratigraphiquc, paléoécologique. *Annales de Paléontologie (Invertébrés)* 66(2): 67–134.

GARDNER, J., 1933. Thc Midway Group ol Tcxas. *University of Texas Bulletin* 3301: 403 p., 28 pls.

GLIBERT, M. & VAN DE POEL, L., 1965. Les Bivalvia fossiles du Cénozoiquc étrangcr des Collections dc l'Institut royal des Scicnces naturelles de Belgiquc. II *Institut Royal des Sciences naturelles de Belgique Mémoires* 78: 105 p.

GLIBERT, M. & VAN DE POEL, L., 1970. Les Bivalvia fossilcs du Cénozoique étranger des Collections de l'Institut royal des Sciences naturelles de Belgique. VI *Institut Royal des Sciences naturelles de Belgique Mémoires* 84: 185 p.

GLIBERT, M. & VAN DE POEL, L., 1973. Les Bivalvia du Danien ct du Montian de Belgiquc. *Institut Royal des Sciences naturelles de Belgique Mémoires* 175: 89 p., 8 pls.

IREDALE, T., 1939. Mollusca Part 1. *British Museum (Natural IIistory) Great Barrier Reef Expedition 1928–29 Scientific Reports* 5(6): 425 p., 5 pls.

KAUFFMAN, E. G., 1969. Form, function, and cvolution. In *Treatise on Invertebrate Paleontology*, C. Teichert, ed., N Mollusca 6, vol. 1: N129–205.

KENLEY, P. R., 1951. Marinc Eocene sediments near Casterton, Victoria. *Australian Journal of Science* 14: 91–92.

KENLEY, P. R., 1954. Thc occurrence of Cretaceous sediments in south-wcstern Victoria. *Proceedings of the Royal Society of Victoria* 66: 1–16, pl. 1.

KENLEY, P. R., 1971. Cainozoic geology of thc eastern part of the Gambier Embayment, southwestern Victoria. In *The Otway Basin of Southeastern Australia. Special Bulletin, Geological Surveys of South Australia and Victoria*, H. Wopfner and J. G. Douglas, eds, pp. 89–153.

LUDBROOK, N. H., 1973. Distribution and stratigraphic utility of Cenozoic molluscan faunas in southern Australia. *Science Reports of the Tohoku University Spec. vol.* 6: 241–261, pls 24–28.

MAKARENKO, D. E., 1970. Rannepalcotscnovye Mollyuski scvcrnoi Ukrainy (Early Paleocene molluscs of the northcrn Ukraine). Adademiya Nauk Ukrainskoi S.S.R. Institut Gcologichcskikh Nauk, Kiev, 128 p., 22 pls.

McGOWRAN, B., 1964. Foraminifcral cvidence for the Paleocenc agc of the King's Park Shale (Pcrth Basin, Western Australia). *Journal of the Royal Society of Western Australia* 47: 81–86.

McGowran, B., 1965. Two Paleocene foraminiferal faunas from the Wangerrip Group, Pebble Point coastal section, Western Victoria. *Proceedings of the Royal Society of Victoria* 79: 9–74, pls 1–6.

McGowran, B., 1991. Maastrichtian and early Cainozoic, southern Australia; planktonic and foraminiferal biostratigraphy. In *The Cainozoic in Australia, a re-appraisal of the evidence*. M. A. J. Williams, P. De Deckker & A. P. Kershaw, eds. *Geological Society of Australia Special Publication* 18: 79–98.

McCoy, F., 1876. *Prodromus of the Palaeontology of Victoria Decade* 3. Geological Survey of Victoria, Melbourne.

Maxwell, P. A., 1969. Middle Tertiary mollusca from North Otago and South Canterbury, New Zealand. *Transactions of the Royal Society of New Zealand* 6(13): 155–185, 3 pls.

Maxwell, P. A., 1992. Eocene Mollusca from the vicinity of McCulloch's Bridge, Waihao River, South Canterbury, New Zealand: Paleoecology and systematics. *New Zealand Geological Survey Paleontological Bulletin* 65: 280 p., 30 pls.

Moore, E. J., 1983. Tertiary marine Pelecypods of California and Baja California: Nuculidae through Malleidae. *United States Geological Survey Professional Paper* 1228A: 1–108, 27 pls.

Palmer, K. V. W. & Brann, D. C., 1965. Catalogue of the Paleocene and Eocene Mollusca of the southern and eastern United States. Part 1. Pelecypoda, Amphineura, Pteropoda, Scaphopoda, and Cephalopoda. *Bulletins of American Paleontology* 48(218): 443 p, 3 pls.

Panteleev, G. S., 1971. Stratigraphiya i dvustvorchatye Mollyuski Datskikh i Paleotsenovyk otlozhenii Zakaspiya (The stratigraphy and bivalve mollusca of the Danian and Paleocene deposits east of the Caspian Sea). Isdatelstvo Nauka, Moscow.

Ponder, W. F., 1967. Observations on the living animal and mode of life of some New Zealand Erycinacean Bivalves. *Transactions of the Royal Society of New Zealand Zoology* 10(3): 31–32.

Ravn, J. P. J., 1939. Études sur les Mollusques du Paléocène de Copenhague. *Det Kongelige Danske Videnskabernes Selskab. Biologiske Skrifter.* 1(1): 106 p., 4 pls.

Singleton, F. A., 1943. An Eocene molluscan fauna from Victoria. *Proceedings of the Royal Society of Victoria* 55: 267–278, pls 12–13.

Spencer-Jones, D., 1971. Marginal Tertiary deposits of the Tyrendarra Embayment — Grassdale and Hamilton District. In *The Otway Basin of Southeastern Australia. Special Bulletin, Geological Surveys of South Australia and Victoria*, H. Wopfner & J. G. Douglas, eds, 241–249.

Stilwell, J. D., 1993. New Early Paleocene Mollusca from the Wangaloa Formation of South Island, New Zealand. *Journal of Paleontology* 67: 360–369.

Stilwell, J. D. & Zinsmeister, W. J., 1992. Molluscan systematics and biostratigraphy Lower Tertiary La Meseta Formation, Seymour Island, Antarctic Peninsula. *Antarctic Research Series* 55: 192 p., 25 pls.

Teichert, C., 1943. Eocene nautiloids from Victoria. *Proceedings of the Royal Society of Victoria* 55: 257–264, pl. 11.

Thorson, G., 1957. Bottom Communities (Sublittoral or Shallow Shelf). In *Treatise on Marine Ecology and Paleoecology. Memoirs of the Geological Society of America* 67(1), J. W. Hedgpeth, ed., 461–534.

Veevers, J. J., Powell, C. McA. & Roots, S. R., 1991. Review of seafloor spreading around Australia. 1. Synthesis of the patterns of spreading. *Australian Journal of Earth Sciences* 38: 373–389, 15 figs.

Wilkinson, C. S., 1865. Report in *Report of the Director of the Geological Survey of Victoria for the period June 1863 to September 1864. Victoria Votes and Proceedings of the Legislative Assembly* 1864–5/44: 21–23.

Zinsmeister, W. J., 1979. Biogeographic significance of the late Mesozoic and early Tertiary molluscan faunas of Seymour Island (Antarctic Peninsula) to the final breakup of Gondwanaland. In *Historical Biogeography, Plate Tectonics and the changing Environment*, J. Gray & A. J. Boucot, eds, Oregon State University Press, 349–355.

Zinsmeister, W. J., 1983. New late Paleocene molluscs from the Simi Hills, Ventura County, California. *Journal of Paleontology* 57(6): 1282–1303, 4 figs.

Zinsmeister, W. J., 1984. Late Eocene bivalves (Mollusca) from the La Meseta Formation, collected during the 1974–1975 joint Argentine–American Expedition to Seymour Island, Antarctic Peninsula. *Journal of Paleontology* 58(6): 1497–1527, 10 figs.

Zinsmeister, W. J. & Macellari, C. E., 1988. Bivalvia (Mollusca) from Seymour Island, Antarctic Peninsula. *Geological Society of America Memoir* 169: 273–284, 16 figs.

ACRAMAN, SOUTH AUSTRALIA:
AUSTRALIA'S LARGEST METEORITE IMPACT STRUCTURE

GEORGE E. WILLIAMS

Department of Geology and Geophysics, University of Adelaide, Adelaide, South Australia 5005

WILLIAMS, G. E., 1994:12:31. Acraman, South Australia: Australia's largest meteorite impact structure. *Proceedings of the Royal Society of Victoria* 106: 105–127. ISSN 0035-9211.

Acraman, located in the Mesoproterozoic Gawler Range Volcanics (1592 ± 2 Ma) in the Gawler Ranges, South Australia, is the largest known impact structure in Australia. It is notable also as the source of an ejecta horizon of shocked volcanic fragments and melt material in Neoproterozoic (~590 Ma) shales in the Adelaide Geosyncline 220–350 km to the east and in coeval shales in the Officer Basin 470 km to the northwest of Acraman.

The centre of the structure is marked by sparse outcrops of shattered dacite in Lake Acraman within a topographic depression 30 km in diameter. The disrupted bedrock exhibits shatter cones and shock lamellae in quartz grains that indicate shock pressures of up to ~15 GPa. A partly fault-controlled apparent ring of valleys and low-lying country occurs at 85–90 km diameter, and satellite images reveal concentric arcuate features at ~150 km diameter.

Acraman is eroded below the original crater floor. The transient cavity that formed immediately after the impact was probably ~40 km in diameter and ~4 km deep. The central uplift of shock-deformed bedrock is ≥10 km in diameter. The structural rim of the 1.3-km-deep final collapse crater may be marked by the ring structure at 85–90 km diameter. Arcuate features at ~150 km diameter may be fractures marking the outer limit of disturbance.

The Acraman structure could have been formed by the impact of an Earth-crossing chondritic asteroid 4.7 km in diameter and of density 3500 kg/m^3 travelling at 25 km/s. The energy of crater formation was 6×10^{22} J, equivalent to 1.5×10^7 megatons of explosive energy. Ejecta blanketed at least 7×10^5 km^2. An Acraman-sized terrestrial impact of an Earth-crossing asteroid occurs on average every few tens of millions of years.

THE ACRAMAN STRUCTURE in South Australia (Fig. 1; Williams 1986, 1987, 1990) is Australia's largest known meteorite impact scar. Furthermore, Acraman is notable among known terrestrial impact structures in having parts of its widely dispersed distal ejecta-blanket of shattered rock preserved (Gostin et al. 1986).

The study of satellite images played a key role in my discovery of the Acraman structure. In 1979, while studying Landsat images for mineral exploration, I thought that the near-circular shape of Lake Acraman (latitude 32°01′S, longitude 135°26′E) and the surrounding topographic depression in the Gawler Ranges might record a major impact structure. In May 1980 I found intensely shattered Yardea Dacite, of the Mesoproterozoic Gawler Range Volcanics, on low islands within Lake Acraman. Petrographic study in 1980 showed that the shattered rocks contain quartz grains with shock lamellae, confirming an impact event. Although the structure was eroded below the former crater floor, it seemed likely that the crater had been at least 30 km in diameter, about the width of the topographic depression containing Lake Acraman. As such, Acraman was the largest impact structure known in Australia.
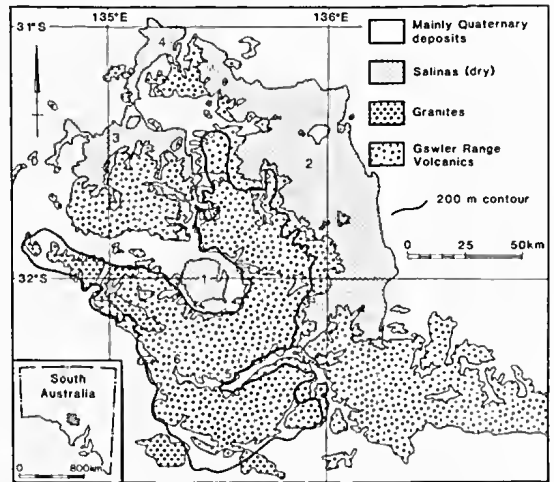
Fig. 1. Geological map of the Gawler Ranges region, South Australia, showing distribution of the Mesoproterozoic Gawler Range Volcanics and coeval granites. 1, Lake Acraman, within the Acraman depression; 2, Lake Gairdner; 3, Lake Everard; 4, Lake Harris; 5, the Yardea corridor, part of an apparent ring structure at 85–90 km diameter; 6, locality of strongly jointed Eucarro Dacite. The generalised 200-m contour is taken from the Port Augusta and Tarcoola topographic sheets (1 : 1 000 000).

In 1985, V. A. Gostin (University of Adelaide) told me of his discovery of volcanic rock fragments, interpreted as impact ejecta, in marine shales of the Neoproterozoic (~590 Ma) Bunyeroo Formation in the Flinders Ranges ~300 km east of Lake Acraman. Blocks of ejecta matched, both in general rock type and degree of shock metamorphism displayed, shattered rocks I had collected from Lake Acraman in 1980. Importantly, the connection between Acraman and the ejecta was indicated by U-Pb zircon ages of ejecta material determined by W. Compston and co-workers at the Australian National University. The wide extent of the ejecta horizon supported my conclusion that a major impact had occurred at Acraman; coarse ejecta must have fallen well beyond the western shore of the gulf-like Adelaide Geosyncline then occupying the position of the Flinders Ranges, to be preserved in muds on the sea floor.

NOAA satellite thermal infrared images of South Australia, newly available in 1985, showed Acraman as a conspicuous 'bullseye' ringed structure, with arcuate features at ~30, 85-90 and ~150 km diameter. The dimensions of the structure suggested that Acraman may rank with the largest impact structures recognised.

This paper reviews the geology and geophysics of the Acraman structure, and discusses the energetics and regional implications of the Neoproterozoic Acraman impact event.

REGIONAL GEOLOGY OF THE GAWLER RANGES

The Acraman impact structure (Fig. 1) lies almost entirely within the Gawler Range Volcanics, a Mesoproterozoic continental suite of mainly acid lavas and ash flows with an exposed thickness of 1 km in the Gawler Ranges (Rutland et al. 1981; Blissett 1986; Fanning et al. 1988; Giles 1988; Creaser & White 1991). The flat-lying, undeformed volcanics now cover more than 25 000 km² and outlying remnants indicate that formerly the suite was much more extensive. Gravity modelling suggests that the volcanics have a full thickness of ~4 km (Zhiqun Shi, pers. commun., 1992).

The Yardea Dacite, the uppermost and most widespread formation of the Gawler Range Volcanics (Creaser & White 1991), crops out continuously over 12 000 km²; it has an exposed thickness of 250 m but probably is much thicker, and an unknown thickness has been removed by erosion. The Yardea Dacite is a highly porphyritic dacite grading to rhyodacite, with phenocrysts of plagioclase, alkali feldspar and hornblende typically 1-3 mm across, as well as augite, pigeonite and rare quartz, in a finely granular red brown or purplish brown microcrystalline matrix. An extensive 'black dacite' marks the base of the formation south of Lake Acraman. The Yardea Dacite shows remarkable mineralogical and geochemical homogeneity over its outcrop area, and ranks as one of the largest felsic volcanic units known.

Arcuate patterns as much as tens of kilometres across in the Gawler Range Volcanics, with volcanic units gently dipping inward, have been interpreted as evidence of cauldron subsidence or a caldera origin (Crawford 1963; Turner 1975; Giles 1977; Branch 1978; Rutland et al. 1981). However, Creaser & White (1991) suggested that no unequivocal evidence for volcanism of the 'caldera-collapse-resurgence' type is known from the Gawler Range Volcanics.

U-Pb zircon geochronology indicates an age of 1592 ± 3 Ma for the black Yardea Dacite and a pooled age of 1592 ± 2 Ma for extrusion of the Gawler Range Volcanics (Fanning et al. 1988). Granites of the Hiltaba Supersuite were intruded at 1585 ± 16 Ma (U-Pb zircon dating; Creaser 1989). The intrusion of the basic Gairdner dyke swarm commencing at 1050-1100 Ma was the last significant magmatic event in the Gawler Ranges region, and marks the earliest phase of rifting associated with the formation of the Adelaide Geosyncline (Parker et al. 1987).

Few earthquakes have been located in the Lake Acraman region, the International Seismological Centre listing only four small events within 90 km of Lake Acraman during 1964-1982. This low rate of seismic activity accords with the finding of Solomon & Duxbury (1987) that impact-induced faults do not long persist as lithospheric zones of weakness.

GEOMORPHOLOGY

Major geomorphological features of the Gawler Ranges region are revealed by digital elevation images (Fig. 2) and a map of the Lake Acraman area (Fig. 3).

The Lake Acraman salina (~20 km diameter, elevation 133-138 m) is eccentrically placed within a near-circular low-lying area 30 km across, termed here the 'Acraman depression' (140-200 m elevation). Except on the northwest, the depression is ringed by the Gawler Ranges that rise up to 300 m above the lake bed. This high ground, as outlined by the generalised 200 m contour (Fig. 1), forms an annulus 25-30 km wide that is breached in the northwest. The Gawler Ranges are bordered to the east and north by a low-lying area that contains the Lake Gairdner salina (113-121 m);
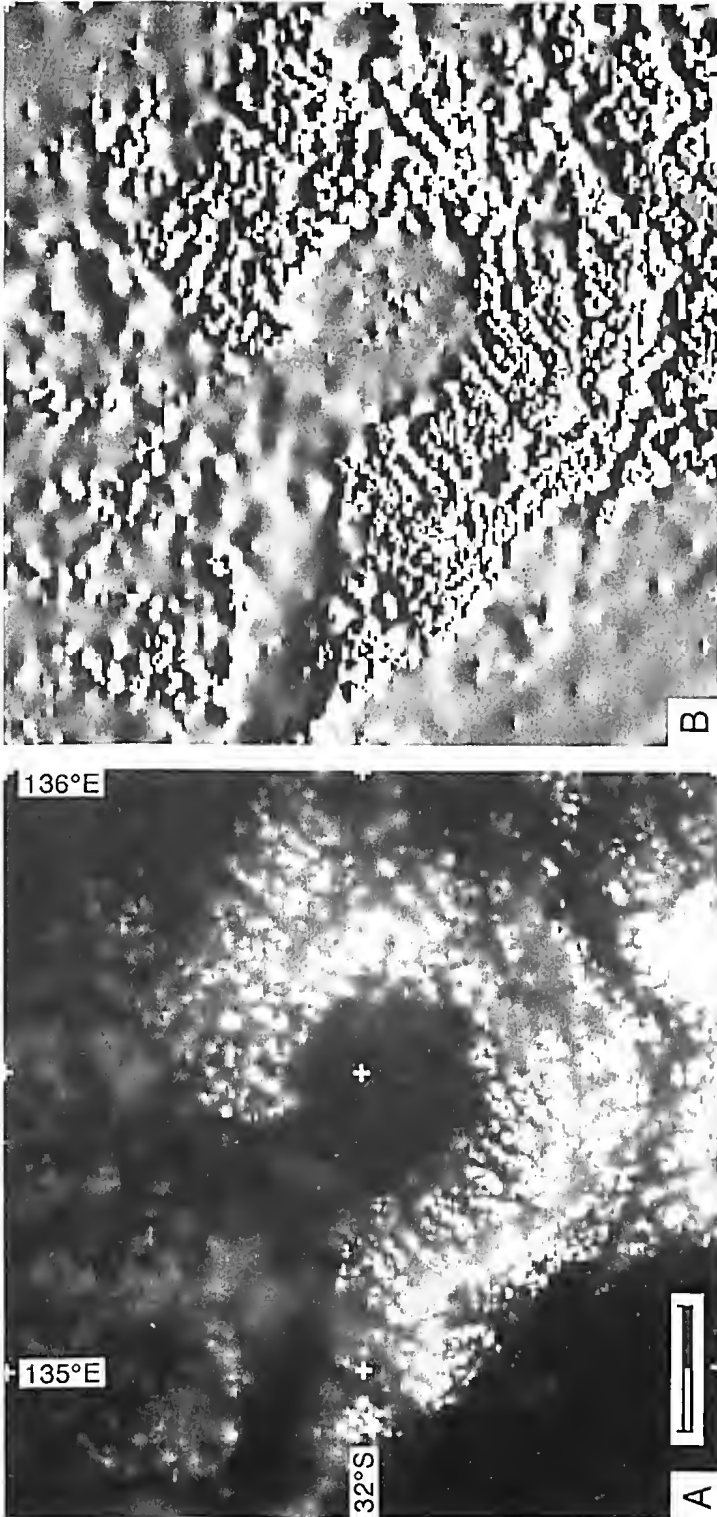
Fig. 2. Digital elevation images of the Gawler Ranges region, South Australia. (A) Grey scale image (light = high elevations, dark = low elevations) showing the Acraman depression surrounded by an annulus of elevated country, and the Yardea corridor at 85–90 km diameter. Scale bar 20 km. (B) Same area as (A) with gradients illuminated from the south, showing a cluster of small peaks near the centre of the Acraman depression, and the Yardea corridor. Images derived from data supplied by the Australian Surveying and Land Information Group and reproduced with the permission of the General Manager, AUSLIG, Department of Administrative Services, Canberra. Data processed by BHP Minerals Exploration Department, Melbourne.

Fig. 4. View looking south across the dry bed of Lake Acraman, with the Gawler Ranges on the skyline.
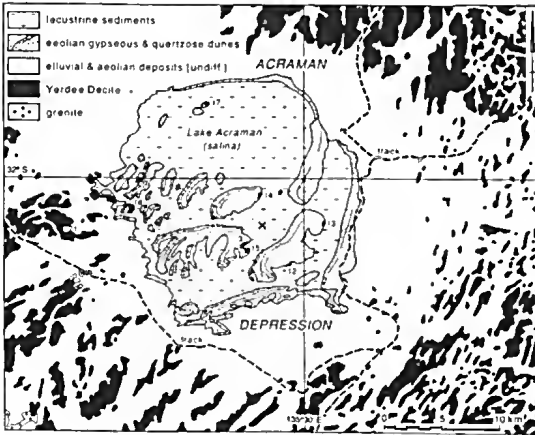
Fig. 3. Geological map of the Acraman depression (= inner topographic depression of the Acraman structure), showing: the outcrop pattern of Yardea Dacite and granite in the Gawler Ranges; the general distribution of Quaternary lacustrine, aeolian and alluvial deposits; field localities, with numbers; and the position of the dipolar aeromagnetic anomaly in the central area of Acraman (cross). Modified from Blissett (1977) and Blissett et al. (1988), with outcrops of Yardea Dacite within Lake Acraman mapped by the present author. To protect rock outcrops, the area of the Acraman depression has been declared a Geological Monument of the Geological Society of Australia, and the Acraman structure is on the Indicative List of Australian sites for inclusion in the UNESCO Global Inventory of Geological and Fossil Sites.

low country that includes the Lake Everard and Lake Harris salinas (121–124 m) lies to the northwest. The Gawler Ranges are flanked on the south and west by subdued terrain (90–200 m) marked by seif dunes and scattered small salinas.

The topography reflects the strong influence of structure sculptured by several cycles of erosion since Mesozoic time. A high-level summit surface of Cretaceous age—the Nott Surface (Twidale et al. 1976)—has elevations of 430–450 m south of Lake Aeraman and 300–330 m north of that lake. The surface was initiated by weathering of a peneplain in Jurassic time; stripping of the regolith and formation of the Nott Surface as a high-level ctch surface were caused by northward tilting of the peneplain during the Early Cretaceous (Campbell & Twidale 1991). The Nott Surface is now dissected to depths as great as 250 m below summit levels in the Gawler Ranges south of Lake Aeraman and to a depth of 150 m north of the lake.
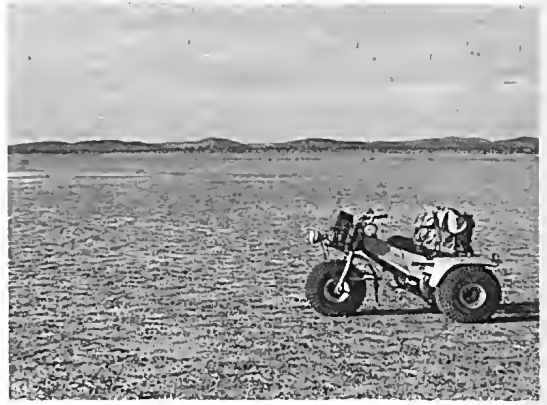
The surface of the Acraman depression (Fig. 3) slopes gently inward from an elevation of 180–200 m at the base of the surrounding ranges to 140 m near the margin of Lake Acraman. The depression is underlain by weathered Yardea Dacite mantled by Miocene–?Early Pliocene ferruginous and siliceous duricrusts as well as by Pleistocene and Holocene alluvium and colluvium (see Blissett et al. 1988). This duricrusted plain formed during the Tertiary and may be compared to Tertiary surfaces that floor valleys elsewhere in the Gawler Ranges (see Twidale et al. 1976). During the Tertiary, drainage found an outlet via the low-lying country (≤150 m elevation) northwest of Lake Acraman and thence northward along a palaeodrainage course now marked by the Lake Everard–Lake Harris chain of salinas (Fig. 1).

The bed of Lake Acraman is as much as 6 m below the level of the adjacent plain; the distant ranges surrounding the lake on most sides (Fig. 4) give the impression of a vast amphitheatre. Like other salinas in southern Australia, Lake Aeraman developed by aeolian deflation during Pleistocene arid intervals (see Bowler 1986). The lake is now a closed basin where saline ground waters crop out, and is floored by damp, sulphidic clays usually veneered by a thin (millimetre) crust of sodium chloride. Under the action of prevailing westerly winds during the Pleistocene, clay, quartz sand and fine-grained gypsum from the lake bed were built into a series of mainly gypseous dunes rising to 30 m above the lake bed on the upwind (western and northwestern) margins of islands. An arcuate bordering dune or lunette rising to 25 m above the lake bed also was built at the eastern and south-

eastern margin of the lake. Low outcrops of intensely shattered dacite are restricted to the lee (eastern) side of several islands in the south-eastern part of Lake Acraman near the centre of the Acraman depression.

Dissection of the Nott Surface has been strongly influenced by joints and structural lineaments in the Gawler Range Volcanics (Fig. 5). The dominant regional trend of joint-controlled valleys in the Yardea Dacite is northeast, with other trends between north and northwest. In addition, several linear structural 'corridors' 3–10 km wide, marked by subdued outcrop and small depressions with salinas, traverse the Gawler Ranges region (Fig. 5). The intersection of two lineaments with the palaeo-drainage outlet northwest of Lake Acraman accounts for the paucity of outcrop in that area. The joint and fracture patterns in the volcanics evidently are of great antiquity, having influenced the form of a palaeosurface buried by Meso-proterozoic (1400 Ma) sandstones in the eastern Gawler Ranges (Campbell & Twidale 1991). The Gairdner dyke swarm parallels the northwest-trending fractures.

The 'Yardea corridor' (Williams 1986) 30 km south of the Acraman depression comprises several near-linear valleys as much as 3 km wide that together extend for at least 70 km roughly con-centric with the southern margin of the depression (Figs 1 and 2). A fault follows the Yardea corridor for 35 km (Blissett 1987; Blissett et al. 1988), but the history of movement on the fault is unknown.

SATELLITE IMAGES OF THE ACRAMAN STRUCTURE

The Acraman structure is clearly revealed by visible spectrum and infrared satellite images. In particular, satellite infrared images, by distin-guishing small differences in surface temperature, can highlight regional structures such as faults, fractures and palaeodrainage courses that are not readily seen on visible spectrum images and photographs.

A Landsat image of most of the Acraman structure (Fig. 5) shows an inner depression (the Acraman depression) and part of an intermediate 'ring' stucture, which includes the Yardea corridor, at 85–90 km diameter. An arcuate feature also is evident at ~150 km diameter, extending 170 km from the southeastern corner of Lake Gairdner northwestward to Lake Everard. West of this feature the bed of Lake Gairdner appears to be crossed by numerous shallow channels containing surface water, in contrast to the dry lake bed to the east. Drilling in Lake Gairdner (Johns 1968)

revealed a salt crust as much as 450 mm thick and abundant halite and gypsum in lake sediments to depths of 14 m west of the arc, but only silt at least 3 m thick with no salt crust to the east. Johns (p. 74) noted that the salt crust 'thinned abruptly' eastward from a locality near the arc. The apparent change in character of the lake deposits across the arc through Lake Gairdner suggests that the line may follow basement faults or buried topography, with generally deeper bedrock to the west. Geophysical studies might test these interpretations.

A NOAA-AVHRR (National Oceanographic and Atmospheric Administration Advanced Very High Resolution Radiometer) satellite thermal infrared night image of northern South Australia (Fig. 6) reveals Acraman as a conspicuous ringed structure. The inner depression is largely encircled by the intermediate 'ring' at 85–90 km diameter; these features appear cooler (darker) possibly because of greater vegetative cover promoted by higher soil moisture. This ring comprises several near-linear features 30–40 km long that together produce a polygonal outline. A break in the ring occurs northwest of Lake Acraman where other lineaments coincide with the palaeodrainage out-let; the palaeodrainage line may be influenced by a north-trending structure. Arcuate features at ~150 km diameter include a line running through lakes Gairdner and Everard, and possibly the southern limit of the Gawler Ranges south of Lake Acraman. The NOAA image also shows several lineaments unrelated to the Acraman structure.

Hence, satellite images support topographic evidence (Figs 1 and 2) that the main geomorph-ological elements of the Gawler Ranges are centred on the Acraman depression. This regional arrange-ment is unrelated to the stratigraphy of the Gawler Range Volcanics.

SHATTERING AND SHOCK METAMORPHISM

Shattered rocks in the central area

Good outcrop of intensely shattered and shocked Yardea Dacite occurs at three localities (Fig. 3, locs 3, 12, 15) on two islands in the southeastern part of Lake Acraman near the centre of the Acraman depression. Poor outcrop of shattered dacite occurs at localities 13 and 14.

The better outcrops display several fracture patterns. Typically the dacite contains numerous closely spaced (millimetre to centimetre), randomly-oriented fractures that produce an irregular mosaic of rock fragments (Fig. 7A). Intense shattering

locally has produced a breccia of finely crushed dacite that may contain fragments of less fractured rock (Fig. 7B).

Near-parallel fractures up to 50 mm apart locally produce platy fragments arranged roughly perpendicular to shallow-dipping joints in the dacite. A reticulate fracture pattern is produced over small areas by groups of near-perpendicular fracture planes 10–20 mm apart.

Broken surfaces of disrupted dacite commonly display striae that locally form small shatter cones (Fig. 7C). Larger shatter cones up to 150 mm long also occur, but are too few to provide reliable structural data. The shatter cones are not as well formed as those developed in fine-grained sedimentary rocks in other impact structures (e.g. Milton 1977).

Fractured rocks outside the central area

Outcrops of fractured Yardea Dacite occur at the margins of islands near the northern and western shores of Lake Acraman (Fig. 3, locs 17, 18). The fracturing does not approach the intensity of disruption in the central area, and shatter cones have not been observed.

Rocks outside the Acraman depression in general are not unusually fractured and shatter cones have not been observed. Isolated outcrops of Yardea Dacite within the Yardea corridor display numerous closely spaced (~50 mm) near-vertical joints which strike northwest obliquely across the trend of the corridor. The jointing may reflect fault movement at the corridor margin.

Outcrop of Euearro Dacite stratigraphically below the Yardea Dacite 23 km northwest of Yardea Homestead (Fig. 1) is strongly jointed and has variable magnetic properties (Blissett et al. 1989). Joints are closely spaced (≤10 mm) and display near-horizontal and near-vertical attitudes. Near-vertical joints locally produce a reticulate pattern like that in the central area of Acraman. Curved joint sets also are present, but shatter cones have not been observed. These disturbed rocks occur near the intermediate ring structure at 85–90 km diameter.

Petrography of the shattered rocks

Yardea Dacite from the central area contains phenocrysts of plagioclase and very minor K-feldspar up to 3 mm long in a fine-grained matrix of K-feldspar intergrown with granular to myrmekitic quartz. Finely divided iron oxide gives the feldspars a red brown colour.

All the shattered rocks studied show microscopic evidence of fracturing and deformation. The fractures, which occur in feldspar phenocrysts and matrix, are defined by limonite-lined veinlets and zones of clear, recrystallised felsic minerals. Several wider fractures contain irregular voids partly lined with clear authigenic feldspar. Some feldspar phenocrysts in the more strongly deformed rocks have highly fractured and deformed shapes showing localised granulation and microbreccia textures. Zircon and apatite grains are greatly fractured. A brown micaceous mineral identified by XRD as stilpnomelane occurs on some fracture surfaces.

From 5–90% of quartz grains in thin-sections of shattered dacite from localities 3 and 15 and rare quartz grains in specimens from locality 12 exhibit closely spaced, parallel planar lamellae, decorated with cavities and finely divided material, that do not transgress grain boundaries (Fig. 7D). As many as four different sets of lamellae have been observed in the same grain. These planar features are identical to the shock lamellae developed in quartz grains in impactites (Robertson et al. 1968). The attitudes of 54 sets of lamellae seen in thin sections of two samples from locality 3, and measured with a universal stage, indicate ω {$10\bar{1}3$} (dominant) and ξ {$11\bar{2}2$} crystallographic orientations, and a high-angle set (70–80°) that may be Υ {$40\bar{4}1$} (Fig. 8). Lamellae densities range from 300–600 per millimetre. These features indicate Type C shock deformation of Robertson et al. (1968) and shock pressures of ~15 GPa (see Robertson & Grieve 1977). Closely spaced shock lamellae in one or more sets occur also in some feldspars in the shattered dacite.

Because of the paucity of outcrop in Lake Acraman and the surrounding depression, the true dimensions of the central area of intense shattering and shock metamorphism cannot be determined,

Fig. 5. Landsat image covering most of the Acraman structure, showing: 1, Lake Acraman within the Acraman depression; 2, Lake Gairdner; 3, Lake Everard; 4, the Yardea corridor at 85–90 km diameter. Surface water (darker areas) in Lake Gairdner helps define an arcuate trend (5) that continues westward to Lake Everard and may mark the outer limit of disturbance at ~150 km diameter. The Gawler Range Volcanics shows strong jointing, and a northwest-trending structural lineament occurs on the northern side of Lake Acraman. A Tertiary palaeodrainage course runs northward from the northwestern margin of the Acraman depression via a chain of small salinas and Lake Everard. Landsat scene 15 February 1973, scene centre S31-30 E135-51; processed by BHP Minerals Exploration Department, Melbourne.
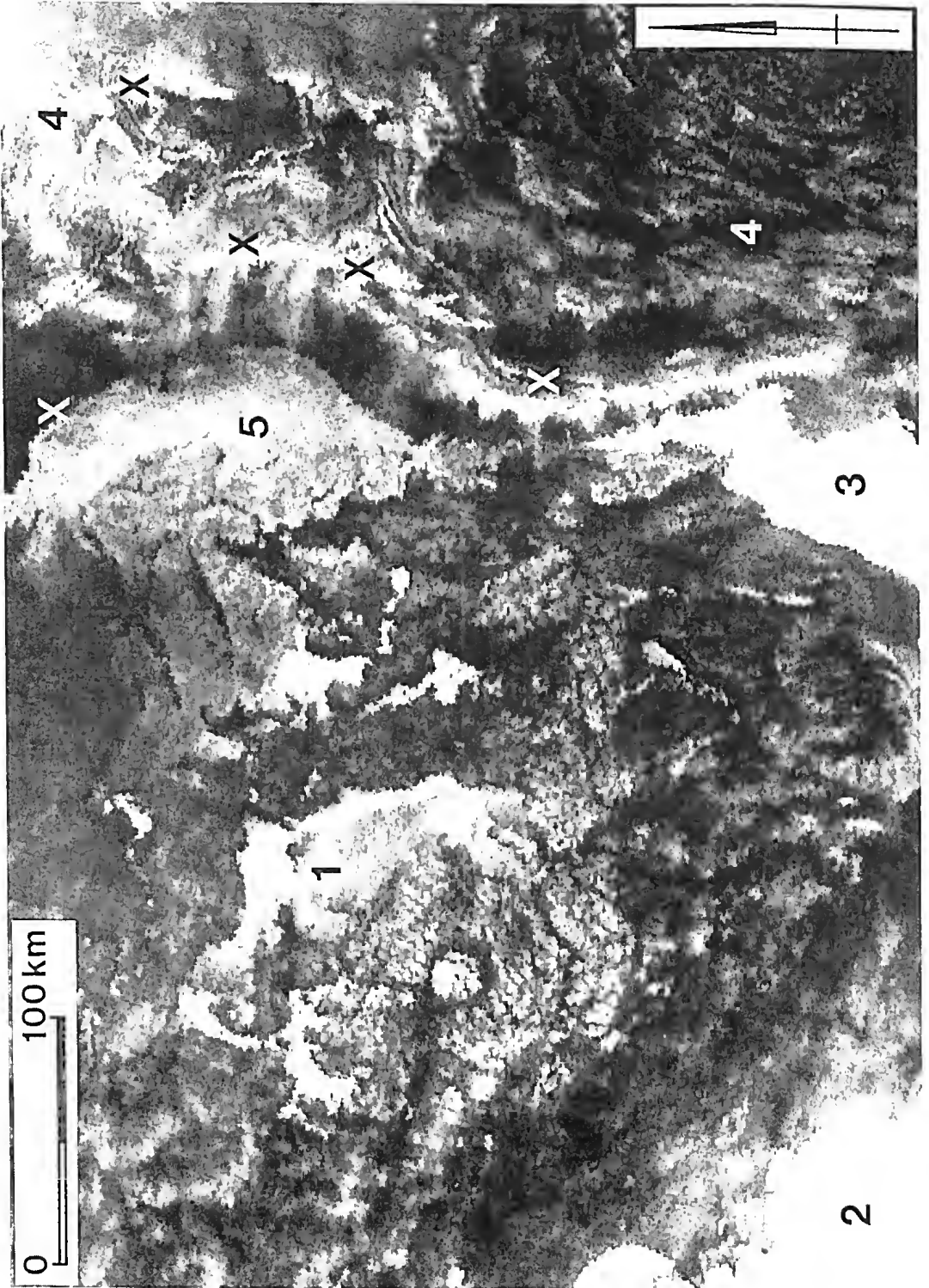
but a minimum diameter of 10 km is suggested by the sparse outcrop. Rocks outside the central area show little if any microscopic evidence of fracturing or deformation, and shock lamellae have not been observed in quartz or feldspar grains.

IMPACT MELT

Outcrop of melt rock (basement rock melted by the impact) at locality 15 in the central area appears to be part of a gently-dipping dyke 1.5 m thick that occurs along a strike length of ~300 m. The melt rock is aphanitic and usually red brown in colour, weathering to buff hues, and is unshattered. Inclusions of dacite range from small xenocrysts of feldspar and partly resorbed xenoliths to blocks of shattered rock as much as 200 mm across; overall, however, the melt rock contains <15% inclusions. The contact with the dacite is marked by irregular-shaped, partly resorbed dacite xenoliths (Fig. 7E) or intensely shattered dacite microbreccia.

Petrography, and XRD and electron-microprobe analyses show that the melt rock consists mainly of slender, twinned, skeletal laths of albite as large as 350×20 μm and commonly arranged in radial quench textures, set in a matrix of cloudy K-feldspar and finely intergrown quartz (Fig. 7F). The matrix also contains finely dispersed iron oxide, as well as scattered larger euhedral grains of variably oxidised titaniferous magnetite up to 30 μm in diameter. Partly resorbed xenoliths comprise microcrystalline aggregates of quartz, K-feldspar and fine-grained cloudy material, and commonly have a reaction rim of titaniferous magnetite grains. Rare corroded quartz xenocrysts display single or multiple sets of shock lamellae.

Microprobe analyses indicate that the Na- and K-feldspar phases in the melt rock have virtually pure, end-member compositions (Ab_{99} and Or_{98}; Table 1). Such compositions indicate that they are low-temperature feldspars (see Kastner & Siever 1979; Boles 1982) formed by secondary alteration of the melt rock, rather than high-temperature equilibrium products of a melt derived from the Gawler Range Volcanics (see Carmichael et al.

1974). The albite laths are the result of low-temperature albitisation of a primary high-temperature feldspar. The matrix K-feldspar and finely intergrown quartz may be devitrification products of glassy material.

The fine-grained, generally inclusion-poor nature of the melt rock, the characteristic quench textures, the presence of shocked-deformed inclusions of quartz, and its limited outcrop within the central area of intensely shattered rocks are all consistent with the melt rock being a dyke or sill below the crater floor (see Dence 1971; Grieve et al. 1977). There is no geological or aeromagnetic evidence that the melt rock represents part of a widespread melt pool in an annulus around a central uplift.

GEOCHEMISTRY

Analyses of undisturbed Yardea Dacite from many localities in the Gawler Ranges, and of shattered Yardea Dacite, dacite microbreccia, and melt rock from the central area at Acraman, are given in Table 2. The Yardea Dacite has a remarkably uniform composition over much of its area, most samples containing from 66% to 69% SiO_2 (Creaser & White 1991). No important difference between the undisturbed and shattered dacite is evident in Table 2; the greater CaO content and LOI for the shattered rocks may indicate their minor secondary alteration.

The three specimens of melt rock assayed show very limited compositional range and have some similarity to the composition of the Yardea Dacite. Apparent trends exist for several elements in the sequence from undisturbed and shattered dacite, through microbreccia, to melt rock. Most notable is the 40–50% increase in potassium content of the melt rock; conversely, the melt rock is depleted slightly in total Fe, MgO and CaO compared with the undisturbed and shattered dacite. Enrichment in potassium and increase in K_2O/Na_2O ratio in melt rock relative to country rock have been observed at other impact sites (Dence 1971; Hartung et al. 1971; Parfenova & Yakovlev 1977; Grieve 1987). A favoured explanation of such potassic enrichment is hydrothermal alteration, particularly

---

Fig. 6. Thermal infrared night image of northern South Australia taken by NOAA satellite. Warm areas including the sea and some salinas appear white, cool areas dark. The Acraman structure appears as a large ringed feature in the western part of the scene, comprising a dark, circular inner area (inner depression) that contains Lake Acraman (paler tone) and concentric features at 85–90 km (dark, polygonal ring) and ~150 km diameter; the ring structure is breached on the northwest by northwest- and north-trending lineaments. Geographic features include: 1, Lake Gairdner; 2, Great Australian Bight; 3, Spencer Gulf; 4, Flinders Ranges; 5, Lake Torrens. Crosses mark main ejecta localities in the Flinders Ranges (northern Adelaide Geosyncline) as much as 350 km from Acraman. NOAA9-AVHRR Band 3, Orbit no. 2246, 21 May 1985, 2200 hours. Image geometrically corrected, Lambert conic conformal projection; processed by BHP Minerals Exploration Department, Melbourne.

of highly shocked felsic clasts, during the impact event.

No important difference exists among trace element values for undisturbed Yardea Dacite, shattered dacite, and melt rock. The values usually do not exceed average abundances for the Earth's crust or acid igneous rocks (see Levinson 1974), although values for Zr, Ba and rare earth elements (La, Ce, Nd) tend to be elevated. A trace element spidergram for undisturbed Yardea Dacite from numerous localities is shown in Fig. 9.

Values for Cr, Co, Ni and platinum-group
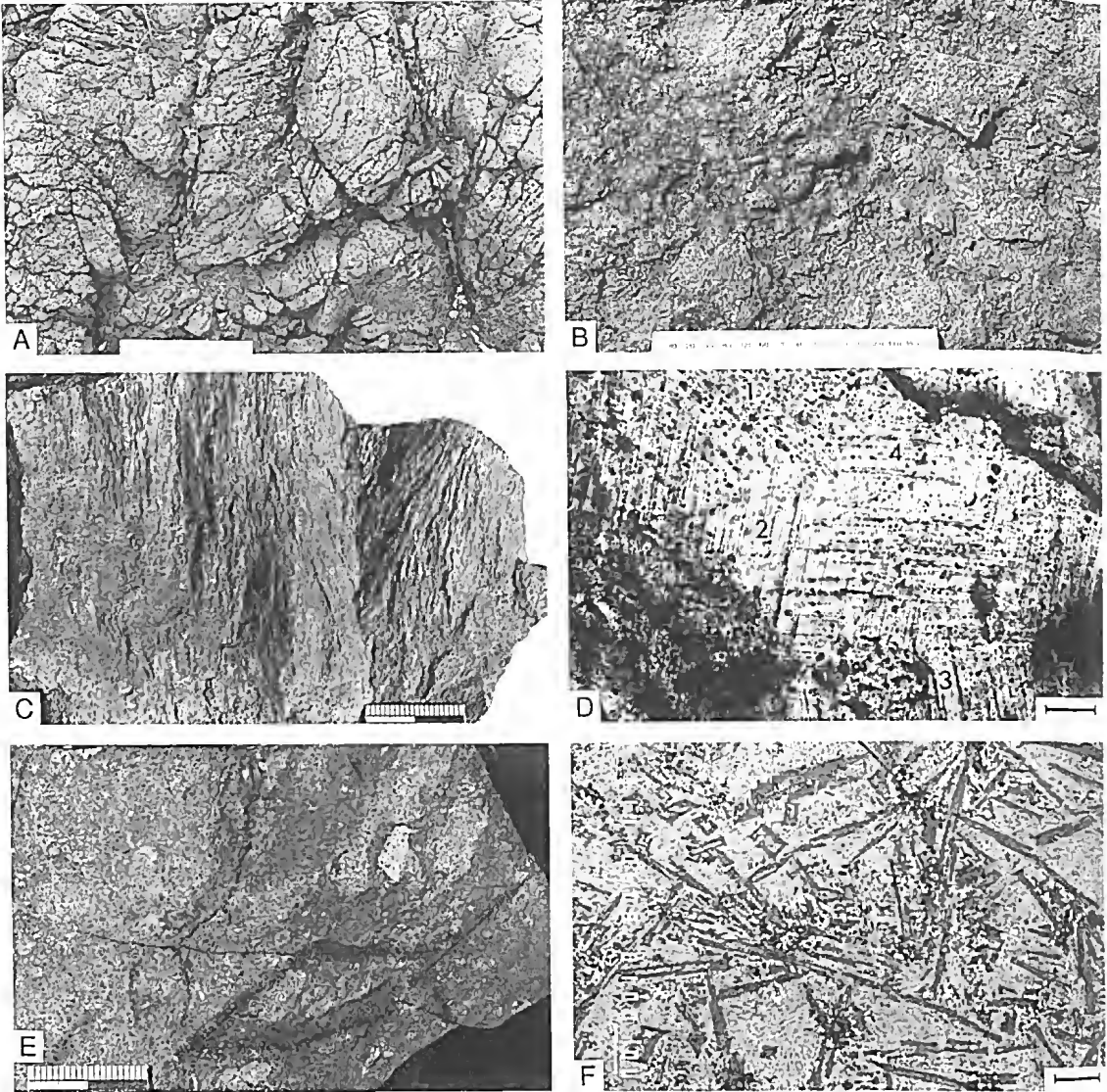
Fig. 7. (A) Strongly fractured Yardea Dacite bedrock, locality 12; scale 150 mm. (B) Brecciated Yardea Dacite, locality 12; scale 150 mm. (C) Broken surface of disrupted Yardea Dacite showing striae and small shatter cone, locality 3; scale 20 mm. (D) Four sets of decorated shock lamellae in a quartz grain from disrupted Yardea Dacite, locality 3; crossed polars, scale bar 25 μm. Sets 1, 2 and 3 parallel to ω crystallographic orientation and set 4 probably parallel to Υ. (E) Disrupted Yardea Dacite (left) and melt rock (darker rock on right), with partly resorbed xenoliths of dacite at the contact, locality 15; scale 20 mm. (F) Electron probe photomicrograph of melt rock from locality 15, showing skeletal laths of albite in a devitrified matrix of K-feldspar (pale) and quartz (darker flecks); scattered grains of iron oxide appear white, black spots are voids. Scale bar 100 μm.
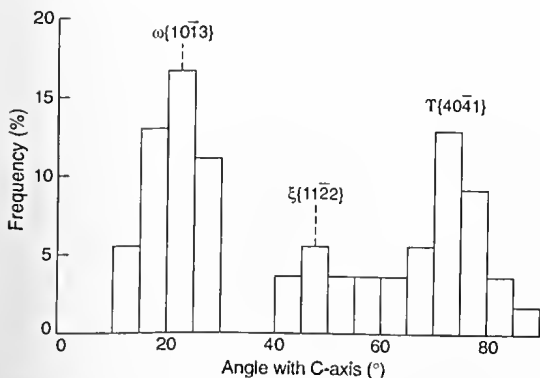
Fig. 8. Frequency histogram for the angle (in degrees) between the c-axis and the pole of 54 sets of shock lamellae in quartz grains in shattered Yardea Dacite, locality 3, central Acraman structure. Crystallographic orientations typical of Type C shock deformation (shock pressures ~15 GPa) in shock-deformed quartz are shown.

	Laths (21)	Matrix (17)	Xenoliths (2)
SiO_2	69.73 ± 0.38	66.14 ± 0.79	67.29
Al_2O_3	19.44 ± 0.17	17.86 ± 0.42	16.99
K_2O	0.12 ± 0.05	15.57 ± 0.53	14.98
Na_2O	10.53 ± 0.50	0.32 ± 0.19	0.47
CaO	0.09 ± 0.08	—	—
MgO	0.03	—	0.20
FeO	0.04	0.12	—
Cl	0.01	—	—

Table 1. Electron microprobe analyses of feldspar phases in melt rock from locality 15, central Acraman structure. Values shown are means (with $\pm 1\sigma$ where applicable) obtained from analyses summed to 100%. Number of analyses in brackets. JEOL 733 Microprobe facility, Electron Optical Centre, University of Adelaide.
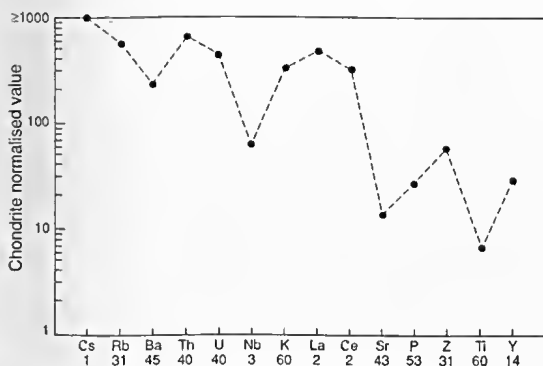
Fig. 9. Trace element spidergram for the Yardea Dacite from numerous localities; the figures below the elements give number of analyses. After Blissett et al. (1989).

elements (PGEs) for shattered dacite and melt rock are not significantly different from values for undisturbed Yardea Dacite. All samples assayed have negligible PGE values. Rocks from several other major impact structures likewise show no anomalous Cr, Co, Ni (Currie & Shafiquallah 1968) and Ir (Palme 1982). The lack of anomalous cosmogenic siderophile elements in the shattered dacite and melt rock at Acraman may reflect erosion to a level well below the former crater floor.

GEOPHYSICAL SIGNATURE

Gravity

The Bouguer gravity anomaly signature for the Gawler Ranges region (Fig. 10) is dominated by several positive anomalies that together form a broad gravity high of amplitude ~20 mGal and 150×100 km in extent that approximates the main area of outcrop of the Gawler Range Volcanics. This broad positive anomaly may reflect more dense, basic rocks at a depth between ~4 and ~12 km (D. Boyd & Zhiqun Shi, pers. commun., 1992).

Most structural and topographic features within the Gawler Ranges cannot be related to the Bouguer gravity signature. The notable exception is the Acraman depression, which is covered by a near-circular negative anomaly of ~6 mGal amplitude and 30–35 km in diameter within a broader gravity low (as much as 10–15 mGal amplitude and ~50 km across). The arcuate features at 85–90 and ~150 km diameter appear unrelated to the regional gravity signature.

Near-circular negative gravity anomalies commonly are associated with impact structures (Pilkington & Grieve 1992), reflecting fractured and brecciated material of lower density than the surrounding undisturbed rocks. No central gravity high such as are displayed by some large impact structures has been identified at Acraman, although the wide gravity-station spacing usually of 5 to 8 km does not permit detailed resolution of the gravity signature.

Density differences between hand specimens of undisturbed Yardea Dacite (mean density 2660 kg/m^3) and shattered dacite from the centre of Acraman range from 0 to 150 kg/m^3, and between undisturbed Yardea Dacite and melt rock from 160 to 240 kg/m^3. Precise modelling of the negative gravity anomaly over Acraman is limited by the wide station spacing, but the anomaly is consistent with disrupted material extending to a depth of at least 5 km beneath the Acraman depression, possibly into underlying denser rocks (Zhiqun Shi, pers. commun., 1992).

	Yardea Dacite*	Yardea Dacite[†]	Shattered Yardea Dacite[§]	Microbrecciated Yardea Dacite**	Melt rock[††]
SiO_2 (%)	67.69 (60)	67.8 (2)	66.1 (3)	70.4	68.6 (3)
TiO_2	0.70 (60)	0.67 (2)	0.76 (3)	0.83	0.83 (3)
Al_2O_3	13.68 (60)	13.5 (2)	13.4 (3)	12.7	14.6 (3)
$Fe_2O_3{}^{§§}$	3.18 (59)	5.02 (2)	5.18 (3)	3.13	2.53 (3)
FeO	2.90 (38)	—	—	—	—
MnO	0.16 (60)	0.12 (2)	0.23 (3)	0.03	0.03 (3)
MgO	1.12 (60)	0.91 (2)	0.73 (3)	0.46	0.36 (3)
CaO	1.66 (60)	1.32 (2)	2.99 (3)	0.29	0.29 (3)
Na_2O	2.95 (60)	3.01 (2)	3.72 (3)	2.27	2.85 (3)
K_2O	4.98 (60)	5.27 (2)	4.65 (3)	6.75	7.30 (3)
P_2O_5	0.28 (53)	0.17 (2)	0.17 (3)	0.25	0.19 (3)
LOl	1.21 (20)	1.90 (2)	2.63 (3)	2.05	2.55 (3)
Cr (ppm)	29 (41)	47 (2)	73 (4)	72	58 (3)
Co	15 (41)	7 (2)	9 (5)	6	6 (3)
Ni	12 (39)	6 (2)	10 (4)	8	5 (2)
Cu	22 (41)	16 (2)	28 (5)	5	10 (3)
Zn	97 (41)	96 (2)	86 (5)	22	26 (3)
Pb	52 (38)	12 (2)	25 (5)	22	20 (3)
V	38 (43)	19	39	—	—
Rb	205 (31)	200 (2)	188 (4)	180	182 (3)
Sr	160 (43)	145 (2)	195 (4)	270	317 (3)
Ba	1631 (45)	1360 (2)	1254 (5)	1840	817 (3)
Zr	406 (31)	417 (2)	373 (4)	420	433 (3)
Nb	22 (3)	23 (2)	20 (4)	22	23 (3)
U	6 (40)	—	—	—	—
Th	28 (40)	28	25	—	—
Ga	—	20	18	—	—
Sc	13 (2)	10	12	<20	<20 (3)
Y	55 (14)	60 (2)	38 (5)	26	24 (3)
La	79 (2)	80	78 (4)	110	130 (3)
Ce	142 (2)	148 (2)	110 (5)	120	177 (3)
Nd	—	60 (2)	57 (4)	<20	63 (3)
Pd*** (ppb)	—	0.78	0.61	—	0.31 (3)
Pt	—	0.84	0.62	—	1.03 (3)
Au	—	0.19	0.14	—	0.13 (3)
Ir	—	<0.005	<0.005	—	0.01 (3)
Ru	—	—	—	—	0.11 (3)

Table 2. Whole rock analytical data for Yardea Dacite, and shattered dacite and melt rock from the Acraman impact structure. (*Note:* Where mean values are given, the number of samples analysed is shown in brackets.) * Undisturbed Yardea Dacite from all areas; data from Blissett et al. (1989). [†]Undisturbed Yardea Dacite from locality 21, 6 km west of Lake Acraman (see Fig. 3). One sample analysed by Classic Comlabs, Adelaide, using XRF and wet chemistry. Values for other sample by courtesy of M. W. Wallace, R. R. Keays and V. A. Gostin. [§]Samples from localities 3, 12 and 15, central area of Acraman, analysed by Classic Comlabs, Adelaide, using XRF and wet chemistry. Additional trace element and PGE values for one sample from locality 12, by courtesy of M. W. Wallace, R. R. Keays and V. A. Gostin. ** Sample from locality 15, analysed by Classic Comlabs, Adelaide, using XRF and wet chemistry. [††]Three samples from locality 15, analysed by Classic Comlabs, Adelaide, using XRF and wet chemistry. PGE values for three samples from locality 15, by courtesy of M. W. Wallace, R. R. Keays and V. A. Gostin. [§§]Total Fe as Fe_2O_3 where no FeO value given. *** Pd, Pt, Au, Ir and Ru values by courtesy of R. R. Keays, M. W. Wallace and V. A. Gostin; analysed by fire assay and neutron activation (see also Gostin et al. 1989).

Fig. 11. Aeromagnetic map for the central area of the Acraman structure, showing a dipolar magnetic anomaly between islands (stippled) in Lake Acraman (cf. Fig. 3). The anomaly indicates a shallow magnetic source. Total magnetic intensity was recorded continuously at an altitude of 152 m along the flight lines shown. Contour interval 50 gammas. Modified from Hiltaba 1:63 360 Aeromagnetic Map of Total Intensity, South Australian Department of Mines and Energy, Adelaide, 1961.

Fig. 10. Bouguer gravity anomaly map of the Gawler Ranges region, showing a negative anomaly centred on the Acraman depression (stippled, except for Lake Acraman). The partly fault-controlled Yardea corridor (stippled, F marks fault) in the south appears unrelated to the gravity signature. Contour interval 1 mGal. L = gravity low. Small crosses mark gravity stations. The large cross in Lake Acraman marks the position of the dipolar aeromagnetic anomaly in the central area (Fig. 11). Recontoured from gravity readings taken by the South Australian Department of Mines and Energy (cf. Yardea and Gairdner 1:250 000 Bouguer Anomaly Maps, South Australian Department of Mines and Energy, Adelaide, 1972).

Aeromagnetics

The most common magnetic signature associated with impact structures is a magnetic low with subdued magnetic relief caused by a reduction in susceptibility; numerous structures also exhibit a central high-amplitude anomaly (Pilkington & Grieve 1992). High-resolution digital aeromagnetic data (400 m line spacing, 80 m ground clearance) for the Gawler Craton, released by the South Australian Department of Mines and Energy in December 1993, show that Acraman is marked by a circular magnetic low as much as 30 km in diameter exhibiting subdued magnetic relief and a central high-amplitude dipolar anomaly. The magnetic low and subdued magnetic relief are most conspicuous for the innermost 20 km diameter, and the full extent of the subdued signature approx-

imates the limits of the Acraman depression and the presumed present extent of fractured Yardea Dacite. The central anomaly (Fig. 11) is at least +200/−150 gammas in amplitude and indicates a shallow (∼300 m depth) magnetic source. The data also indicate the presence of northwest- and northeast-trending faults along the line of the Yardea corridor to the south of the area of subdued magnetic signature.

Specimens of fractured dacite from within the Acraman depression on average show a 70% decrease in magnetic susceptibility compared with those of undisturbed Yardea Dacite; this observation suggests that the subdued magnetic signature at Acraman indeed reflects a decrease in susceptibility. The melt rock has a mean magnetic susceptibility nearly twice that of undisturbed Yardea Dacite.

The presence of the circular magnetic low with subdued magnetic relief and the reduced magnetic susceptibility of the shattered dacite strongly support an impact origin for Acraman. Furthermore, the central anomaly at Acraman equates with the central high-amplitude magnetic anomaly displayed

by many impact structures, including all those >40 km in diameter (see Pilkington & Grieve 1992). The central anomaly at Acraman may reflect basic igneous rocks brought from great depth by structural uplift (see following), or a concentration of melt rock or melt-bearing breccia. The lack of other aeromagnetic anomalies at Acraman attributable to the edges of a melt sheet suggests, however, that melt material in general is not widely distributed.

PALAEOMAGNETISM

Palaeomagnetic study of the Acraman structure (Schmidt & Williams 1991) aimed to constrain the age of the impact and test the postulated correlation of the Acraman impact and deposition of the ejecta horizon in the Bunyeroo Formation in the Adelaide Geosyncline.

Samples for palaeomagnetic analysis comprised shattered dacite (locs 3, 12) and melt rock (loc. 15) from the central area, and undisturbed dacite from as far as 20 km south of the Acraman depression. Only the melt rock responded to magnetic cleaning, and carried a remanent magnetisation that was stable to 630°C. This observation, the coercivity of remanence, and XRD and microprobe analyses indicate that the magnetic carrier is partially oxidised titanomagnetite. That carrier is likely to have retained an original magnetic direction from the time of the impact.

The directions of the high-temperature components from eight prepared specimens of melt rock, and their mean direction and error circle (declination = 48.3°, inclination $I = 54.7°$, $\alpha_{95} = 5.2°$) yield a mean pole position at 8.6°S latitude and 353.4°E longitude ($A_{95} = 6.3°$). The character of the melt-rock remanence, such as low directional dispersion and high stability, is similar to that displayed by impactites containing melt material from other impact structures (e.g. Larochelle & Currie 1967; Pohl 1971; Pohl & Soffel 1971).

The direction of magnetisation of the melt rock is unlike the palaeomagnetic direction found in the Gawler Range Volcanics (see Chamalaun & Dempsey 1978). Furthermore, there is no sign of a present field direction attributable to weathering, or viscous remanent magnetisation (although a lightning-induced component may have obliterated the latter). It is thus concluded that the high-temperature component of the magnetisation dates from the time of cooling immediately after the impact. The indicated pole for the melt rock must be considered a virtual geomagnetic pole (VGP) because the geomagnetic field direction recorded at the time of cooling is an instantaneous sample of a geomagnetic field direction subject to secular variation.

The Neoproterozoic Bunyeroo Formation containing the ejecta horizon is a fine-grained red shale of marine-shelf origin, ideal for palaeomagnetic analysis. The direction of the cleaned magnetisation component of the Bunyeroo Formation was acquired prior to folding of the formation during the Cambro-Ordovician Delamerian Orogeny (McWilliams & McElhinny 1980), which is evidence that its remanence may be original and date from about the time the strata were deposited. The presence of both normal and reverse magnetisations within the Bunyeroo Formation further suggests that the magnetisation is primary, because most overprints are of a single polarity. Indeed, the Bunyeroo palaeomagnetic data satisfy six of the seven 'reliability criteria' for palaeomagnetic data, including a field test, given by Van der Voo (1990).

The pole for the Bunyeroo Formation (McWilliams & McElhinny 1980) is at 7°S latitude and 17°E longitude ($I = -40°$, $A_{95} = 12°$), and may be considered a palaeomagnetic pole (*sensu stricto*) at about the time of deposition. As shown in Fig. 12, this pole is very close to the VGP for the Acraman melt rock, and is quite distinct from probable Delamerian overprint poles for ~450 Ma.
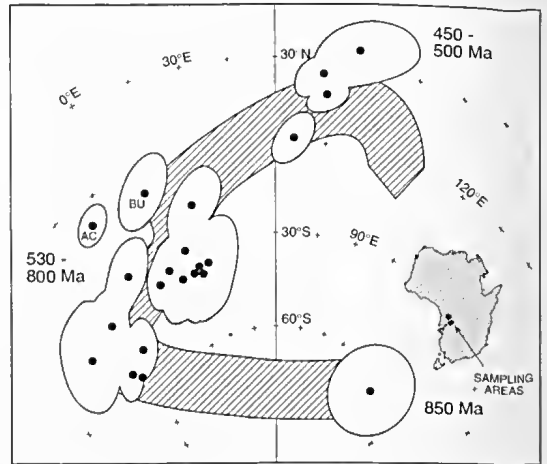
Fig. 12. Pole path (striped) for the Adelaide Geosyncline Gawler–Craton region of South Australia for the interval 850–450 Ma. Solid dots are palaeomagnetic poles mostly determined for strata in the Adelaide Geosyncline (shown with polar error ellipses of 95% confidence). BU, palaeomagnetic pole for the Bunyeroo Formation; AC, virtual geomagnetic pole for melt rock from Acraman. Modified from McWilliams & McElhinny (1980) with additional data from Schmidt & Williams (1991).

statistical tests show that the Acraman VGP may be regarded as a subset of the Bunyeroo palaeomagnetic pole position (Schmidt & Williams 1991), indicating that the two pole positions are statistically indistinguishable. This agreement strongly supports the postulate that the ejecta horizon in the Bunyeroo Formation was derived from Acraman.

The Acraman VGP indicates an instantaneous palaeomagnetic latitude of $35.2 \pm 6.3°$, and the Bunyeroo palaeomagnetic pole a palaeolatitude of $22.8 \pm 12.0°$. These data imply that the Acraman impact occurred in low to moderate palaeolatitudes.

GEOCHRONOLOGY

K/Ar and $^{40}Ar/^{39}Ar$ analysis

Conventional K/Ar and $^{40}Ar/^{39}Ar$ total fusion and step heat experiments were performed on two samples of melt rock from locality 15 in an attempt to directly determine the age of the impact (Baldwin et al. 1991). The samples were typical of the melt rock, consisting mainly of albite laths in a devitrified matrix of cloudy K-feldspar and quartz.

An estimate of the apparent age of the melt rock is ~450 Ma, Late Ordovician. Because the feldspars in the melt rock evidently formed as a result of low-temperature authigenic replacement and devitrification, the apparent age is regarded as a *minimum* age for the impact. The apparent age therefore may record the time elapsed since formation of the low-temperature feldspar phases. It may be concluded that the apparent age of ~450 Ma reflects secondary processes rather than the impact event itself.

It is noteworthy that eight K/Ar apparent ages determined for melt rock from the Brent impact structure in Canada averaged only 342 Ma (range 301–414 Ma), much less than the inferred stratigraphic age of 450–500 Ma (Hartung et al. 1971); the melt rock apparent ages for Brent were regarded as minima because of some argon loss subsequent to the impact. The findings for Acraman and Brent indicate that K/Ar and $^{40}Ar/^{39}Ar$ ages for melt rock from degraded, very old (particularly Precambrian) impact structures should be interpreted with caution because the rock dated probably would be exhumed (former depths $\geqslant 2$ km) and may have undergone diagenetic changes such as authigenic replacement of fine-grained feldspars and devitrification of glass.

Apatite fission track analysis

One sample of melt rock (3 kg) and one of shattered Yardea Dacite (4 kg) from localities 15 and 3, respectively, in the central area of Acraman were examined by I. R. Duddy (Geotrack International, Melbourne) for possible fission track dating of zircon, sphene and apatite in an attempt to constrain the age of the Acraman impact. Neither sample yielded sufficient grains of zircon or sphene for reliable fission track analysis, and no apatite was obtained from the melt rock. Sufficient apatite grains for fission track analysis were, however, obtained from the shattered dacite, although the grains were very shattered.

An apatite fission track apparent age of 319 ± 19 Ma is indicated for shattered Yardea Dacite from locality 3 (Table 3). The apparent age agrees with other apatite fission track apparent ages determined by Ferguson (1981) for the Gawler Craton in South Australia (mean of 13 ages = 331 ± 30 Ma, 1σ).

A first-order interpretation of the apatite fission track apparent age is that the sample was at a temperature of $100 \pm 20°C$, the apatite track retention temperature (Moore et al. 1986), at ~320 Ma. The unimodal, negatively skewed distribution of fission track lengths for apatite from the shattered dacite (Fig. 13) is characteristic of areas that have had a steady 'slow-cooling' type of thermal history (see Gleadow et al. 1986). Assuming the apparent age reflects a 'slow-cooling' history, the amount of erosion since 320 Ma could, in principle, be estimated if the palaeogeothermal gradient were known. Conversely, if the maximum amount of erosion since that time were known it would be possible to estimate a minimum palaeogeothermal gradient.

Sample	Number of grains	Spontaneous track density ($\times 10^6$ cm^{-2})	Induced track density ($\times 10^6$ cm^{-2})	Correlation coefficient	Apparent age $\pm 1\sigma$ (Ma)
WAC-3/1	21	1.731 (811)*	1.076 (504)*	0.873	319 ± 19

Table 3. Apatite fission track analytical results for shattered Yardea Dacite, locality 3, central Acraman structure. Data by courtesy of I. R. Duddy, Geotrack International, Melbourne. *Number of tracks counted shown in brackets.

Taking the apatite track retention temperature to be $100 \pm 20°C$, a mean surface palaeotemperature of 20°C and a 'normal' palaeogeothermal gradient in the range 20–30°C/km (the average geothermal gradient determined for the Gawler Craton is 20–25°C/km; Cull & Conley 1983), the slow-cooling interpretation of the apparent age would seem to require erosion of 2–5 km since 320 Ma. Alternatively, a higher geothermal gradient may have affected the Gawler Craton during the mid-Carboniferous, when the apatite 'clock' was reset at shallower depth. Independent evidence for rates of erosion on the Gawler Craton, or for a regional thermal event during the late Palaeozoic, would be required to discriminate between these two interpretations. In view of evidence for widespread orogenic and thermal activity in central Australia and South Australia during the late Palaeozoic (e.g. Li et al. 1989; Camacho et al. 1991; Idnurm & Heinrich 1993), which may have produced an above-normal palaeogeothermal gradient ($\geq 30°C/km$) for the Gawler Craton, the apatite fission track data are perhaps best regarded as indicating a *maximum* of ~2 km of erosion at Acraman since 320 Ma.

Fig. 13. Frequency histogram of fission track lengths in apatite for shattered Yardea Dacite, locality 3, central Acraman structure. Mean track length, $13.78 \pm 0.15 \mu m$; standard deviation of distribution, $1.04 \mu m$; skewness, −0.203; kurtosis, 2.944; number of tracks measured, 50. Data courtesy of I. R. Duddy (Geotrack International, Melbourne).

DISCUSSION – THE ACRAMAN IMPACT EVENT

Evidence for an impact origin of the Acraman structure

Acraman displays numerous criteria for the identification of impact structures (Table 4). Indeed, the Acraman structure qualifies on all criteria given by Dence (1972) for the identification of terrestrial

Criterion (after Dence 1972; Pilkington and Grieve 1992)	Acraman structure
1. Presence of meteorites: rare except in ejecta of *young* craters.	Distal, shocked ejecta with Ir anomaly preserved in Neoproterozoic strata.
2. Circular plan, particularly near centre.	Circular inner topographic depression 30 km in diameter.
3. Rim structure, including disturbed zone or peripheral trough, in complex craters.	Apparent ring structures at 85–90 km and ~150 km diameter.
4. Central structure, with central uplift in complex craters.	'Single peak' central uplift area ≥ 10 km diameter.
5. Generally negative gravity anomaly.	~6 mGal negative gravity anomaly 30–35 km across associated with the inner topographic depression.
6. Magnetic field variable, commonly subdued. Central magnetic anomaly.	Subdued aeromagnetic signature over inner topographic depression. Dipolar aeromagnetic anomaly in central area.
7. Crater rocks show lower seismic velocities than surrounding rocks.	Seismic data not available.
8. Brecciation observed in outcrop and subsurface.	Rocks of central uplift area intensely shattered and brecciated.
9. Shock metamorphism indicated by shatter cones, shock lamellae in minerals, melt rock, mixed breccias, high-pressure phases.	Shatter cones, multiple sets of shock lamellae in quartz and feldspar grains, melt rock, mixed melt rock and breccia, present in central uplift area.

Table 4. Criteria for the identification of impact structures compared with features displayed by the Acraman structure.

impact structures (excluding young craters) except for his criterion no. 7 (low seismic velocities), seismic data not being available. In addition, Acraman is notable among known terrestrial impact structures in evidently having part of its distal ejecta blanket of rock fragments preserved (Gostin et al. 1986; Compston et al. 1987; Wallace et al. 1989, 1990c). This ejecta horizon is anomalous in cosmogenic siderophile elements, including Ir (Gostin et al. 1989; Wallace et al. 1990b, 1990c), and locally contains abundant altered tektite-like spherules and shard-like clasts (Wallace et al. 1990a). These observations together leave no reasonable doubt that the Acraman structure is of impact origin.

Age of the impact

Dating techniques have not provided a direct estimate of the age of the Acraman impact. The most that can be concluded, from the K/Ar and ^{40}Ar/^{39}Ar data, is that the impact occurred *at least* 450 million years ago. The likely age of the impact is, however, provided by stratigraphy. Much data together argue strongly that Acraman is the source of the ejecta horizon near the base the Neoproterozoic Bunyeroo Formation in the Adelaide Geosyncline and the correlative Rodda Beds in the Officer Basin (Gostin et al. 1986, 1989; Wallace et al. 1989, 1990c):

1. All large fragments (pebble to boulder size) and sand-grade clastic material in the ejecta were derived from pink to red felsic volcanic rocks similar to the Yardea Dacite at Acraman.

2. Comparable shattering and shock pressures (up to ~15 GPa) are displayed by ejecta clasts and shattered Yardea Dacite in the central area at Acraman.

3. Shattered euhedral zircons from ejecta clasts gave a U-Pb age of 1575 ± 11 Ma (Compston et al. 1987), which is nearly concordant with the U-Pb zircon age of 1592 ± 3 Ma for the Yardea Dacite (Fanning et al. 1988). The slightly younger age for the ejecta may indicate derivation of material from a higher stratigraphic level than that of the dacite now exposed at the impact site, or possible lead loss due to shock resetting.

4. The geographic distribution of the preserved ejecta horizon (Fig. 14) and the regional variation of ejecta clast size (Wallace et al. 1990c) are consistent with Acraman as the source.

5. Palaeomagnetic data support correlation of the Acraman impact and deposition of the ejecta horizon in the Bunyeroo Formation (Schmidt & Williams 1991).
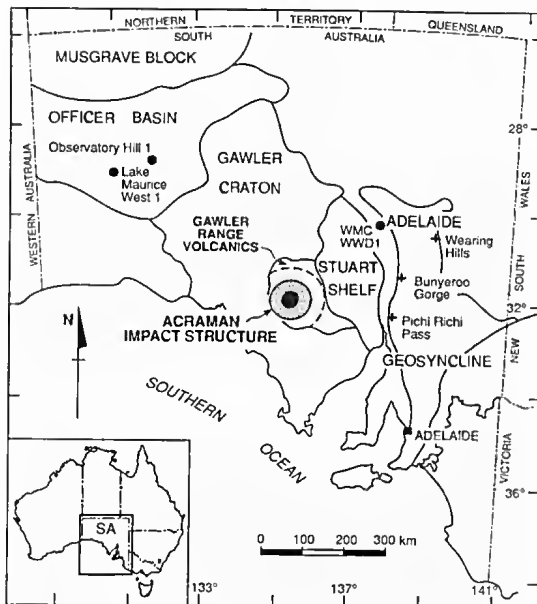
Fig. 14. Map of South Australia showing the Acraman impact structure and the main localities of the related ejecta horizon in the Adelaide Geosyncline and Officer Basin. Crosses indicate ejecta recorded in outcrop of the Bunyeroo Formation, small solid dots ejecta in core from drill holes (see Gostin et al. 1986; Wallace et al. 1989, 1990c).

Hence, determination of the age of the Bunyeroo Formation should provide the age of the Acraman impact. The Yarloo Shale, the equivalent of the Bunyeroo Formation on the Stuart Shelf (Fig. 14), gave a Rb-Sr total rock age of 588 ± 35 Ma (Webb et al. 1983). Combined Rb-Sr total rock data for the Yarloo Shale and subjacent shales gave a mean age of 593 ± 32 Ma (Compston et al. 1987). Thus, the age of the Bunyeroo Formation may be approximated as 590 Ma. A late Neoproterozoic age is consistent with the advanced degradation of Acraman.

The interpretation of such Rb-Sr total rock data is complicated by the possible effects of inherited detrital mica and subsequent diagenesis. According to the Neoproterozoic stratigraphy of Harland et al. (1990, p. 29), the Bunyeroo Formation forms the lowermost unit of the Wonokan Stage of the Ediacara Epoch; Harland et al. (1990) place the base of the Wonokan at 590 Ma, some 20 million years older than their estimate of 570 Ma for the base of the Cambrian. However, recent time-scales incorporating the latest U-Pb zircon ages place the base of the Cambrian at 540 Ma (Odin & Odin

GEORGE E. WILLIAMS

1990; Young & Claoué-Long 1991). Hence, the age of the Bunyeroo Formation and its ejecta horizon may prove to be as young as 560 Ma.

Depth of erosion since the impact

Acraman displays 'erosional level 7' of Grieve & Robertson (1979), which they define as 'crater floor removed, substructure exposed'. The peak recorded shock pressure of ~15 GPa for bedrock exposed at the centre of Acraman is lower than the expected 25–30 GPa at the centre of terrestrial complex structures (see Grieve 1988), indicating erosion at Acraman to a level below the autochthonous crater floor.

The depth of erosion since the impact may be estimated by several methods. The 'slow cooling' interpretation of the apatite fission track data may indicate as much as 2 km of erosion since 320 Ma, assuming an above-normal palaeogeothermal gradient ($\geq 30°C/km$) for the region in late Palaeozoic time. Such an erosion rate, if projected over the past 600 m.y., would give as much as 4 km of erosion of the Gawler Range Volcanics since the impact.

Rates of erosion in southern Australia over the past 100–200 m.y., if applicable since 600 Ma, suggest a smaller figure for depth of erosion since the impact. The high-level, Cretaceous Nott Surface in the Gawler Ranges, now dissected to depths of 250 m, is an etch surface likely once mantled by a thick regolith; hence, as much as 350 m of erosion may have occurred in parts of the Gawler Ranges region over the past 100 m.y. Taking this erosion rate of 3.5 m/m.y. as the mean rate of Phanerozoic erosion in the Gawler Ranges region—the Gawler Craton may have been severely eroded during its Permian continental glaciation (see Crowell & Frakes 1971)—some 2 km of erosion since the impact would be indicated.

Because the crater has been removed by erosion, an estimate of crater depth would provide a minimum depth of erosion since the impact. From Pilkington & Grieve (1992), true final depth d_f (from crater rim to base of crater fill) = $0.52 \, D_f^{0.2}$, where D_f is the final crater diameter for crystalline targets. Taking the diameter of the Acraman depression of 30 km as a minimum final crater diameter (as discussed below, the final rim-to-rim diameter may have been greater) gives $d_f = 1.03$ km. Thus, at least 1 km of erosion has occurred since the impact.

Hence, 2 km of erosion and perhaps up to twice that figure may have occurred at Acraman since the impact at ~590 Ma. By comparison, 1.5 to 2 km of erosion probably has occurred near the

centre of the Siljan structure in Sweden since the impact at 368 Ma (Grieve 1988, 1991), indicating an erosion rate at Siljan closer to the lower estimate for Acraman.

Dimensions and structure of the former crater

The dimensions of the former crater at Acraman must be estimated from the extent of disturbed rocks as much as a kilometre or more below the crater floor. Such estimates must be made with caution, for as noted by Grieve (1991), erosional processes on the Earth can enhance, modify or remove original morphological elements of an impact structure.

The diameter of the Acraman depression, which evidently is underlain by fractured rocks, provides a guide to the diameters of the transient cavity and excavated area. However, the relation among shock-wave attenuation rates with depth, the diameters of the transient cavity and excavated area, and the approximate limit of disrupted bedrock varies according to the size of the impactor and the energy of the impact (Dence et al. 1977). Applying the three models of Dence et al. (1977, their fig. 10) to Acraman, the diameters of the transient cavity and excavated area could be as much as 30% greater than the horizontal limits of disrupted bedrock (2 GPa) at the level for 15 GPa central shock-pressure (the maximum shock pressure observed for bedrock outcrop at the centre of Acraman), the estimated adjustment factor depending on the energy of the impact. A minimum diameter of 3.0×10^4 m for the transient cavity/excavated area at Acraman gives an energy $\geq 10^{22}$ J (from Dence et al. 1977), suggesting that an adjustment factor of 30% for cavity diameter may apply. Hence, the transient cavity and excavated area at Acraman may have been as great as 40 km in diameter, 30% greater than the diameter of the Acraman depression. This figure is consistent with the estimate (Grieve 1988) that erosion has reduced the apparent diameter of the excavated area at Siljan, Sweden, by 12–15% for a depth of erosion perhaps only about half that at Acraman.

According to Grieve (1991), the depth of excavation of the transient cavity $d_e \approx 0.1 \, D_t$, where D_t is the diameter of the transient cavity. Taking $D_t = 40$ km for Acraman gives a depth of excavation of ~4 km. Such a depth of excavation is allowable given the present thickness of ~4 km for the Gawler Range Volcanics estimated from gravity data and the possible erosion of 2 km or more of volcanics since the impact.

The centre of the Acraman depression is marked by a dipolar aeromagnetic anomaly, sparse out-

crops of intensely shattered and shock-deformed Yardea Dacite, and an apparent dyke of fine-grained, generally inclusion-poor melt rock. This central area is interpreted as the central uplift, with a diameter $\geqslant 10$ km. According to Melosh (1989), the central uplift of an impact structure forms by wholesale collapse of an initially deep transient cavity, mainly by uplift of rocks below the crater's centre while rim rocks slump downward and inward.

The apparent lack of bounding faults near the margin of the Acraman depression suggests that the final structural rim occurred at a greater diameter. Possibly the final structural rim is marked by the partly fault-controlled ring at 85–90 km diameter; the polygonal shape of this ring feature implies that any final collapse occurred along pre-existing fractures. According to Grieve (1987, 1991), the diameter of obvious excavation of a terrestrial impact structure $D_e = 0.50$–0.65 D_f, and Lakomy (1990) gives the transient cavity diameter $D_t = (0.57 \pm 0.03)D_f$ for seven Phanerozoic impact structures. Figures for the Sudbury structure ($D_t \approx 100$ km and $D_f \approx 150$–200 km; Grieve et al. 1991) are in the ratio 0.50–0.67. The estimates of D_t and $D_e = 40$ km for Acraman and the diameter of the apparent ring at 85–90 km are in the ratio 0.44–0.47; this range approaches the lower limit for other structures, despite the severe degradation of Acraman and the evident influence of prior structure on the location of the ring feature at 85–90 km diameter.

Available data suggest that the pre-erosional form of Acraman was that of a 'central peak crater' (see Melosh 1989). Diameters of the uneroded structural features — central uplift, excavated area, and possible final structural rim — may have been $\geqslant 10$ km, ~40 km, and 85–90 km, respectively. Interestingly, these dimensions are comparable to those of numerous 'protobasins' (large peak plus inner-ring basins) on Mercury and Mars (see Pike & Spudis 1987). A diameter D_f of 85–90 km for the final structural rim would indicate a true depth d_f of 1.3 km after slumping of the crater walls (see Pilkington & Grieve 1992). Arcuate features at ~150 km diameter may be faults or fractures marking the outer limit of disturbance. It is noteworthy that the Manicouagan impact structure in Quebec likewise has an outer topographic ring at ~150 km diameter which may mark the outer limit of disturbance well beyond the final structural rim at 100 km diameter (Dence 1977; Grieve & Head 1983).

Grieve (1991) suggested that $SU = 0.06$ $D_f^{1.1}$, where SU is the observed amount of uplift undergone by the deepest horizon now exposed in the central uplift of a complex structure. According to Pilkington & Grieve (1992), SU also may provide a useful estimate of the depth of the fractured zone. For Acraman, taking $D_f = 85$–90 km gives $SU = 8.0$–8.5 km. This figure suggests that dense basic rocks presumed from gravity data to underlie the Gawler Range Volcanics at a depth between ~4–12 km may now be near the surface in the central uplift. The dipolar magnetic anomaly over the central uplift is consistent with the presence of basic rocks or melt rock at shallow depth. Drilling would be required to determine the source of this anomaly.

Dynamics of the impact

The relationship for crater diameter as a function of impactor diameter and velocity (Schmidt & Holsapple 1982, their fig. 6) indicates that a transient cavity/excavated area 40 km in diameter, as estimated here for Acraman, could have been formed by an impactor 5.5 km in diameter and density 2200 kg/m^3 travelling at 25 km/s. As the geochemistry of the Bunyeroo ejecta layer suggests that the Acraman impactor had a chondritic composition (Gostin et al. 1989; Wallace et al. 1990c), a density of 3500 kg/m^3 is more appropriate, giving an impactor diameter of 4.7 km for a velocity of 25 km/s.

These figures indicate that the Acraman impactor had kinetic energy of 6×10^{22} J, which was converted to explosive energy (equivalent to 1.5×10^7 megatons) on impact. By comparison, the 1-km-diameter Meteor Crater in Arizona had a formation energy $\leqslant 60$ megatons and the largest man-made nuclear detonation was 60 megatons (Melosh 1989).

Acraman shows some evidence of asymmetry in plan. The deepest part of the regional negative gravity anomaly (Fig. 10), the dipolar magnetic anomaly (Fig. 11) and the area of shattered rocks marking the central uplift appear offset 1–2 km south of the centre of the Acraman depression (Fig. 3). Furthermore, the 85–90-km ring structure is most clearly expressed in the south as the fault-controlled Yardea corridor (Figs 1, 2 and 10). Because complex craters produced by oblique impact may exhibit an uprange offset of the central peak complex and more extensive rim/wall collapse uprange (Schultz & Gault 1992), the observations for Acraman may suggest oblique impact from the south (south uprange).

Ejecta blanket

The sedimentology, geochemistry and distribution of preserved ejecta from Acraman are discussed

by Gostin et al. (1986, 1989) and Wallace et al. (1989, 1990a, 1990b, 1990c); the main ejecta localities are shown in Fig. 14. The thickness of the ejecta layer in the Adelaide Geosyncline 220–350 km east of Acraman ranges from 0–400 mm, with clasts as much as 300 mm in diameter. Distances given are minima for the time of impact because subsequent folding and reverse faulting within the Geosyncline would have shortened the distances between impact and eastern ejecta sites, possibly by tens of kilometres (Gostin et al. 1986). The sandy ejecta in the Officer Basin 470 km northwest of the impact site, seen only in two drill cores, is <1 mm to 7 mm thick. True thicknesses of ejecta that fell in the Adelaide Geosyncline may be less than maximum recorded thicknesses because of likely resedimentation of ejecta material (see Gostin et al. 1986). The formation of ejecta rays also could cause lateral variation in ejecta thickness. Study of ejecta distribution in the Bunyeroo Formation and Rodda Beds may test the suggestion of oblique impact from the south, although relatively few good exposures of the Bunyeroo Formation are known in the southern Adelaide Geosyncline.

Cratering data (obtained from small-scale laboratory experiments, nuclear and high-explosive craters, terrestrial meteorite impact craters, and estimates for lunar craters) suggest that, over a wide range of scales, ejecta blanket thickness t decreases with distance r from a crater centre as

$$t = 0.14R^{0.74}(r/R)^{-3.0} \text{ for } r \geqslant R \qquad (1)$$

where R is the transient crater radius and all dimensions are in metres (McGetchin et al. 1973). Employing Equation (1), a transient crater radius of 2×10^4 m for Acraman gives a thickness for undisturbed ejecta of 160 mm at a distance of 220 km from the crater centre, a thickness of 40 mm at a radius of 350 km, and a thickness of 16 mm at a radius of 470 km. These estimated thicknesses for an undisturbed ejecta blanket are of the same order as observed thicknesses for the ejecta horizons in the Bunyeroo Formation and Rodda Beds.

At a radius of 470 km, the Acraman ejecta of rock fragments, sand and glassy material would have covered 6.9×10^5 km², nearly three times the area of the United Kingdom. Finer-grained ejecta and dust would have spread much farther, and consequences of the impact could have exerted medium-term (days to months) influence on global climate. McLaren & Goodfellow (1990) concluded that evidence should be sought for an influence of the Acraman impact event on Vendian (late Neoproterozoic) biota and geochemistry.

As observed by Gostin et al. (1989), the unique character of the ejecta derived from Acraman may permit intercontinental correlation of Neoproterozoic sediments. Young (1992) suggested that the most convincing support for the hypothesis that Australia and North America were juxtaposed during the Neoproterozoic would be the discovery of the Acraman ejecta in strata of the northern Canadian Cordillera. The continental reconstruction of Young (1992, his fig. 1) implies that Neoproterozoic deposition in the Canadian Cordillera occurred within 800–1000 km of the Acraman impact site. Taking the transient crater radius for Acraman as 2×10^4 m, Equation (1) indicates that the thickness of an undisturbed ejecta layer would be 3.3 mm at 800 km radius and 1.7 mm at 1000 km. Such potential thicknesses and possible identifiable trace element and rare-earth element geochemical fingerprints of ejecta derived from the Gawler Range Volcanics (see Table 2 and Fig. 9) together may provide a tangible target in any search for the Acraman ejecta horizon within Neoproterozoic shales in the Canadian Cordillera.

EARTH'S CRATERING RECORD

Some 130 terrestrial impact craters and structures are currently recognised, nine of which are >50 km in diameter (Grieve 1991). Acraman could have resulted from impact with a large, Earth-crossing asteroid, there presently being an estimated 2000 such bodies $\geqslant 1$ km in diameter (Ahrens & Harris 1992; Matthews 1992; Shoemaker 1992). According to Shoemaker, the Earth-crossing swarm 'is depleted by collision of some of these asteroids with the planets and by ejection of others from the solar system. The swarm is replenished chiefly by collisional fragmentation of main-belt asteroids and injection of the fragments into Earth-crossing orbits.'

In the present regime, an asteroid >1 km in diameter strikes the Earth and produces a crater >10 km in diameter about once every 100 000 years, on average. An Acraman-sized impact with an Earth-crossing asteroid occurs on average every few tens of millions of years. The Earth also resides in a swarm of comets, members of which also occasionally strike our planet. A comet nucleus >10 km in diameter collides with the Earth and produces a crater >150 km in diameter about once every 100 million years, on average.

As stressed by Shoemaker (1992), impact of asteroids and comets is a *normal geological process* that has persisted throughout Earth history. It is being increasingly acknowledged that this process has had a major influence on the development

of life, at least during the Phanerozoic. Indeed, were it not for the active processes of crosion that have long existed on the Earth and which remove traces of all but the largest impacts in less than 500 million years, our planet would be as pock-marked with impact craters as are the other terrestrial planets.

ACKNOWLEDGEMENTS

REFERENCES

AHRENS, T. J. & HARRIS, A. W., 1992. Deflection and fragmentation of near-Earth asteroids. *Nature* 360: 429–433.

BALDWIN, S. L., McDOUGALL, I. & WILLIAMS, G. E., 1991. K/Ar and ^{40}Ar/^{39}Ar analyses of meltrock from the Acraman impact structure, Gawler Ranges, South Australia. *Australian Journal of Earth Sciences* 38: 291–298.

BLISSETT, A. H., 1977. Gairdner map sheet, 1 : 250 000 Geological Series. South Australian Department of Mines and Energy, Adelaide.

BLISSETT, A. H., 1986. Subdivision of the Gawler Range Volcanics in the Gawler Ranges. *Geological Survey of South Australia Quarterly Geological Notes* 97: 2–11.

BLISSETT, A. H. (comp.), 1987. Geological setting of the Gawler Range Volcanics, Geological Atlas Special Series, 1 : 500 000. South Australian Department of Mines and Energy, Adelaide.

BLISSETT, A. H., PARKER, A. J. & CROOKS, A. F., 1988. Yardea map sheet, 1 : 250 000 Geological Series. South Australian Department of Mines and Energy, Adelaide.

BLISSETT, A. H., PARKER, A. J. & SCHEFFLER, J., 1989. Gawler Ranges excursion, October 7th–9th, 1989. *South Australian Department of Mines and Energy Report Book* 89/70, 47 p.

BOLES, J. R., 1982. Active albitization of plagioclase, Gulf Coast Tertiary. *American Journal of Science* 282: 165–180.

BOWLER, J. M., 1986. Spatial variability and hydrologic evolution of Australian lake basins: analogue for Pleistocene hydrologic change and evaporite formation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 54: 21–41.

BRANCH, C. D., 1978. Evolution of the Middle Pro-terozoic Chandabooka Caldera, Gawler Range acid volcano-plutonic province, South Australia. *Journal of the Geological Society of Australia* 25: 199–216.

CAMACHO, A., SIMONS, B. & SCHMIDT, P. W., 1991. Geological and palaeomagnetic significance of the Kulgera Dyke Swarm, Musgrave Block, NT, Australia. *Geophysical Journal International* 107: 37–45.

CAMPBELL, E. M. & TWIDALE, C. R., 1991. The evo-lution of bornhardts in silicic volcanic rocks in the Gawler Ranges. *Australian Journal of Earth Sciences* 38: 79–93.

CARMICHAEL, I. S. E., TURNER, F. J. & VERHOOGEN, J., 1974. *Igneous Petrology*. McGraw-Hill, New York, 739 p.

CHAMALAUN, F. H. & DEMPSEY, C. E., 1978. Palaeo-magnetism of the Gawler Range Volcanics and implications for the genesis of the Middleback hematite orebodies. *Journal of the Geological Society of Australia* 25: 255–265.

COMPSTON, W., WILLIAMS, I. S., JENKINS, R. J. F., GOSTIN, V. A. & HAINES, P. W., 1987. Zircon age evidence for the Late Precambrian Acraman ejecta blanket. *Australian Journal of Earth Sciences* 34: 435–445.

CRAWFORD, A. R., 1963. Large ring structures in a South Australian Precambrian volcanic complex. *Nature* 197: 140–142.

CREASER, R. A., 1989. The Geology and Petrology of Middle Proterozoic Felsic Magmatism of the Stuart Shelf, South Australia. La Trobe Univer-sity, Melbourne, PhD thesis (unpubl.).

CREASER, R. A. & WHITE, A. J. R., 1991. Yardea Dacite — large-volume, high-temperature felsic volcanism from the Middle Proterozoic of South Australia. *Geology* 19: 48–51.

CROWELL, J. C. & FRAKES, L. A., 1971. Late Paleozoic glaciation: Part IV, Australia. *Geological Society of America Bulletin* 82: 2515–2540.

CULL, J. P. & CONLEY, D., 1983. Geothermal gradients and heat flow in Australian sedimentary basins. *BMR Journal of Australian Geology and Geo-physics* 8: 329–337.

CURRIE, K. L. & SHAFIQULLAH, M., 1968. Geochemistry of some large Canadian craters. *Nature* 218: 457–459.

DENCE, M. R., 1971. Impact melts. *Journal of Geo-physical Research* 76: 5552–5565.

DENCE, M. R., 1972. The nature and significance of terrestrial impact structures. *24th International Geological Congress, Montreal*, Section 15: 77–89.

DENCE, M. R., 1977. The Manicouagan impact structure observed from Skylab. *NASA Report* SP-380: 175–189.

DENCE, M. R., GRIEVE, R. A. F. & ROBERTSON, P. B., 1977. Terrestrial impact structures: principal characteristics and energy considerations. In *Impact and Explosion Cratering*, D. J. Roddy, R. O. Pepin & R. B. Merrill, eds, Pergamon, New York, 247–275.

FANNING, C. M., FLINT, R. B., PARKER, A. J., LUDWIG, K. R. & BLISSETT, A. H., 1988. Refined Proterozoic evolution of the Gawler Craton, South Australia, through U-Pb zircon geochronology. *Precambrian Research* 40/41: 363–386.

FERGUSON, K. U., 1981. Fission Track Dating of Shield Areas, Australia: Relationships Between Tectonic and Thermal Histories and Fission Track Age Distribution. University of Melbourne, MSc thesis, 194 p. (unpubl.).

GILES, C. W., 1977. Rock units in the Gawler Range Volcanies, Lake Everard area, South Australia. *Geological Survey of South Australia Quarterly Geological Notes* 61: 7–16.

GILES, C. W., 1988. Petrogenesis of the Proterozoic Gawler Range Volcanics, South Australia: *Precambrian Research* 40/41: 407–427.

GLEADOW, A. J. W., DUDDY, I. R., GREEN, P. F. & HEGARTY, K. A., 1986. Fission track lengths in the apatite annealing zone and the interpretation of mixed ages. *Earth and Planetary Science Letters* 78: 245–254.

GOSTIN, V. A., HAINES, P. W., JENKINS, R. J. F., COMPSTON, W. & WILLIAMS, I. S., 1986. Impact ejecta horizon within late Precambrian shales, Adelaide Geosyncline, South Australia. *Science* 233: 198–200.

GOSTIN, V. A., KEAYS, R. R. & WALLACE, M. W., 1989. Iridium anomaly from the Acraman impact ejecta horizon: impacts can produce sedimentary iridium peaks. *Nature* 340: 542–544.

GRIEVE, R. A. F., 1987. Terrestrial impact structures. *Annual Review of Earth and Planetary Sciences* 15: 245–270.

GRIEVE, R. A. F., 1988. The formation of large impact structures and constraints on the nature of Siljan. In *Deep Drilling in Crystalline Bedrock, Volume 1: The Deep Gas Drilling in the Siljan Impact Structure, Sweden and Astroblemes*, A. Bodén & K. G. Eriksson, eds, Springer, Berlin, 328–348.

GRIEVE, R. A. F., 1991. Terrestrial impact: the record in the rocks. *Meteoritics* 26: 175–194.

GRIEVE, R. A. F., DENCE, M. R. & ROBERTSON, P. B., 1977. Cratering processes: as interpreted from the occurrence of impact melts. In *Impact and Explosion Cratering*, D. J. Roddy, R. O. Pepin & R. B. Merrill, eds, Pergamon, New York, 791–814.

GRIEVE, R. A. F. & HEAD, J. W., 1983. The Manicouagan impact structure: an analysis of its original dimensions and form. *Proceedings of the 13th Lunar and Planetary Science Conference, Journal of Geophysical Research* 88: suppl. A807–A818.

GRIEVE, R. A. F. & ROBERTSON, P. B., 1979. The terrestrial cratering record. I. Current status of observations. *Icarus* 38: 212–229.

GRIEVE, R. A. F., STÖFFLER, D. & DEUTSCH, A., 1991. The Sudbury structure: controversial or misunderstood? *Journal of Geophysical Research* 96: 22 753–22 764.

HARLAND, W. B., ARMSTRONG, R. L., COX, A. V., CRAIG, L. E., SMITH, A. G. & SMITH, D. G. (eds), 1990. *A Geologic Time Scale 1989*. Cambridge University Press, Cambridge, 263 p.

HARTUNG, J. B., DENCE, M. R. & ADAMS, J. A. S., 1971. Potassium-argon dating of shock-metamorphosed rocks from the Brent impact crater, Ontario, Canada. *Journal of Geophysical Research* 76: 5437–5448.

IDNURM, M. & HEINRICH, C. A., 1993. A palaeomagnetic study of hydrothermal activity and uranium mineralization at Mt Painter, South Australia. *Australian Journal of Earth Sciences* 40: 87–101.

JOHNS, R. K., 1968. Investigation of lakes Torrens and Gairdner. *South Australian Department of Mines Report of Investigations* 31, 90 p.

KASTNER, M. & SIEVER, R., 1979. Low temperature feldspars in sedimentary rocks. *American Journal of Science* 279: 435–479.

LAKOMY, R., 1990. Distribution of impact induced phenomena in complex terrestrial impact structures: implications for transient cavity dimensions. *Proceedings of the Lunar and Planetary Science Conference* 21: 676–677.

LAROCHELLE, A. & CURRIE, K. L., 1967. Paleomagnetic study of igneous rocks from the Manicouagan structure, Quebec. *Journal of Geophysical Research* 72: 4163–4169.

LEVINSON, A. A., 1974. *Introduction to Exploration Geochemistry*. Applied Publishing, Calgary, 612 p.

LI, Z. X., POWELL, C. McA. & SCHMIDT, P. W., 1989. Syn-deformational remanent magnetization of the Mount Eclipse Sandstone, central Australia. *Geophysical Journal International* 99: 205–222.

MATTHEWS, R., 1992. A rocky watch for Earthbound asteroids. *Science* 255: 1204–1205.

McGETCHIN, T. R., SETTLE, M. & HEAD, J. W., 1973. Radial thickness variation in impact crater ejecta: implications for lunar basin deposits. *Earth and Planetary Science Letters* 20: 226–236.

McLAREN, D. J. & GOODFELLOW, W. D., 1990. Geological and biological consequences of giant impacts. *Annual Review of Earth and Planetary Sciences* 18: 123–171.

McWILLIAMS, M. O. & McELHINNY, M. W., 1980. Late Precambrian paleomagnetism of Australia: the Adelaide Geosyncline. *Journal of Geology* 88: 1–26.

MELOSH, H. J., 1989. *Impact Cratering*. Oxford University Press, New York, 245 p.

MILTON, D. J., 1977. Shatter cones — an outstanding problem in shock mechanics. In *Impact and Explosion Cratering*, D. J. Roddy, R. O. Pepin & R. B. Merrill, eds, Pergamon, New York, 703–714.

MOORE, M. E., GLEADOW, A. J. W. & LOVERING, J. F.,

1986. Thermal evolution of rifted continental margins: new evidence from fission tracks in basement apatites from southeastern Australia. *Earth and Planetary Science Letters* 78: 255–270.

ODIN, G.-S. & ODIN, C., 1990. Échelle numérique des temps géologiques. *Bureau de Recherches Géologiques et Minières, Société Géologique de France*, no. 35.

PALME, H., 1982. Identification of projectiles of large terrestrial impact craters and some implications for the interpretation of Ir-rich Cretaceous/Tertiary boundary layers. *Geological Society of America Special Paper* 190: 223–233.

PARFENOVA, O. V. & YAKOVLEV, O. I., 1977. Some peculiarities of selective evaporation in target rocks after meteoritic impact. In *Impact and Explosion Cratering*, D. J. Roddy, R. O. Pepin & R. B. Merrill, eds, Pergamon, New York, 843–859.

PARKER, A. J., RICKWOOD, P. C., BAILLIE, P. W., McCLENAGHAN, M. P., BOYD, D. M., FREEMAN, M. J., PIETSCH, B. A., MURRAY, C. G. & MYERS, J. S., 1987. Mafic dyke swarms of Australia. In *Mafic Dyke Swarms*, H. C. Halls & W. F. Fahrig, eds, *Geological Association of Canada Special Paper* 34: 401–417.

PIKE, R. J. & SPUDIS, P. D., 1987. Basin-ring spacing on the Moon, Mercury, and Mars. *Earth, Moon, and Planets* 39: 129–194.

PILKINGTON, M. & GRIEVE, R. A. F., 1992. The geophysical signature of terrestrial impact structures. *Reviews of Geophysics* 30: 161–181.

POHL, J., 1971. On the origin of the magnetization of impact breccias on Earth. *Zeitschrift für Geophysik* 37: 549–555.

POHL, J. & SOFFEL, H., 1971. Paleomagnetic age determination of the Rochechouart impact structure (France). *Zeitschrift für Geophysik* 37: 857–866.

ROBERTSON, P. B., DENCE, M. R. & VOS, M. A., 1968. Deformation in rock-forming minerals from Canadian craters. In *Shock Metamorphism of Natural Materials*, B. M. French & N. M. Short, eds, Mono Book Corporation, Baltimore, 433–452.

ROBERTSON, P. B. & GRIEVE, R. A. F., 1977. Shock attenuation at terrestrial impact structures. In *Impact and Explosion Cratering*, D. J. Roddy, R. O. Pepin & R. B. Merrill, eds, Pergamon, New York, 687–702.

RUTLAND, R. W. R., PARKER, A. J., PITT, G. M., PREISS, W. V. & MURRELL, B., 1981. The Precambrian of South Australia. In *Precambrian of the Southern Hemisphere*, D. R. Hunter, ed., Elsevier, Amsterdam, 309–360.

SCHMIDT, P. W. & WILLIAMS, G. E., 1991. Palaeomagnetic correlation of the Acraman impact structure and the Late Proterozoic Bunyeroo ejecta horizon, South Australia. *Australian Journal of Earth Sciences* 38: 283–289.

SCHMIDT, R. M. & HOLSAPPLE, K. A., 1982. Estimates of crater size for large-body impact: gravity-scaling results. *Geological Society of America Special Paper* 190: 93–102.

SCHULTZ, P.H. & GAULT, D. E., 1992. Recognizing impactor signatures in the planetary record. In *Large Meteorite Impacts and Planetary Evolution: Lunar and Planetary Institute Contribution* 790: 64–65.

SHOEMAKER, E. M., 1992. Large-body impact is a geologic process. *Geological Society of America Abstracts with Programs* 24: A134.

SOLOMON, S. C. & DUXBURY, E. D., 1987. A test of the longevity of impact-induced faults as preferred sites for later tectonic activity. *Proceedings of the 17th Lunar and Planetary Science Conference, Journal of Geophysical Research* 92 (B4): E759–E768.

TURNER, A. R., 1975. The petrology of the eastern Gawler Range Volcanic Complex. *Geological Survey of South Australia Bulletin* 45, 135 p.

TWIDALE, C. R., BOURNE, J. A. & SMITH, D. M., 1976. Age and origin of palaeosurfaces on Eyre Peninsula and the southern Gawler Ranges, South Australia. *Zeitschrift für Geomorphologie* 20: 28–55.

VAN DER VOO, R., 1990. The reliability of paleomagnetic data. *Tectonophysics* 184: 1–9.

WALLACE, M. W., GOSTIN, V. A. & KEAYS, R. R., 1989. Discovery of the Acraman impact ejecta blanket in the Officer Basin and its stratigraphic significance. *Australian Journal of Earth Sciences* 36: 585–587.

WALLACE, M. W., GOSTIN, V. A. & KEAYS, R. R., 1990a. Spherules and shard-like clasts from the late Proterozoic Acraman impact ejecta horizon, South Australia. *Meteoritics* 25: 161–165.

WALLACE, M. W., GOSTIN, V. A. & KEAYS, R. R., 1990b. Acraman impact ejecta and host shales: evidence for low-temperature mobilization of iridium and other platinoids. *Geology* 18: 132–135.

WALLACE, M. W., WILLIAMS, G. E., GOSTIN, V. A. & KEAYS, R. R., 1990c. The Late Proterozoic Acraman impact — towards an understanding of impact events in the sedimentary record. *Mines and Energy Review, South Australia* 57: 29–35.

WEBB, A. W., COATS, R. P., FANNING, C. M. & FLINT, R. B., 1983. Geochronological framework of the Adelaide Geosyncline. *Geological Society of Australia Abstracts* 10: 7–9.

WILLIAMS, G. E., 1986. The Acraman impact structure: source of ejecta in late Precambrian shales, South Australia. *Science* 233: 200–203.

WILLIAMS, G. E., 1987. The Acraman structure — Australia's largest impact scar. *Search* 18: 143–145.

WILLIAMS, G. E., 1990. The Acraman impact structure, South Australia. *Abstracts for the International Workshop on Meteorite Impact on the Early Earth, Perth, Australia. Lunar and Planetary Institute Contribution* 746: 60–61.

YOUNG, G. & CLAOUÉ-LONG, J., 1991. Age control on sedimentary sequences. *BMR Research Newsletter* 15: 14–16.

YOUNG, G. M., 1992. Late Proterozoic stratigraphy and the Canada–Australia connection. *Geology* 20: 215–218.

ECOLOGY OF *CALOSTEMMA* AND *CRINUM* (AMARYLLIDACEAE) IN THE RIVER MURRAY AREA, SOUTH-EASTERN AUSTRALIA

Tracy Clark & R. F. Parsons

Botany Department, La Trobe University, Bundoora, Victoria 3083

CLARK, T. & PARSONS, R. F., 1994:12:31. Eeology of *Calostemma* and *Crinum* (Amaryllidaeeae) in the River Murray area, south-eastern Australia. *Proceedings of the Royal Society of Victoria* 106: 129–145. ISSN 0035-9211.

Calostemma luteum, *C. purpureum* and *Crinum flaccidum* are the only native plant species in Victoria possessing true bulbs. Their distribution at their southern limit on and near the River Murray floodplain is described. Distribution of *Calostemma* flower colour forms may be related to water dispersal of seed by various rivers entering the Murray. Whilst some stands found follow elevation eontours and may be related to seed dispersal by past very high floods, others are well upslope from the present floodplain.

All three taxa produce large, buoyant, non-dormant, water-rich seeds less than six weeks after flowering. *Calostemma* seeds had more complete germination than *Crinum* at 15°/10°C but not at 25°/15°C in keeping with Calostemma's more temperate range. Watered two-month-old seedlings of both genera produeed small bulbs and roots, whilst unwatered ones produced large bulbs but no roots. In dry storage, all seeds had germinated by two months. At 23 months, all *Calostemma* seedlings were dead but half the *Crinum* seedlings were still alive in keeping with their larger seed size. The burial of the shoot apex by the positively geotropie cotyledon may be an adaptation to protect it from drought.

Young *Crinum* seedlings remained alive and floating after two months in both fresh and seawater; *Calostemma* seedlings remained alive in fresh water but were usually killed by seawater. Mature *Crinum* bulbs contained a number of live, unemerged inflorescences at all sampling dates while in *Calostemma* none were found between March and September, suggesting that flowers are initiated no more than onee per year. The flowering time for both *Crinum* and *Calostemma* was summer-autumn following rain; rains after Mareh produced leaf emergence but no flower emergence. In *Crinum*, even showers as light as 6 mm may produce some flowering; in *Calostemma* 15 mm produeed flowering while 9 mm did not.

Both genera show low leaf palatability to grazing mammals, but predation on seeds by emus and bulbs by pigs has been reported.

WHILE most of Australia's ten native species of Amaryllidaceae occur in well-watered tropical to subtropical areas (Hewson 1987; Telford 1987), *Calostemma luteum, C. purpureum* and *Crinum flaccidum* (Figs 1 and 2) extend into arid and semi-arid parts of inland Australia, reaching as far south as the River Murray area around latitude 34°S. These, and two species of *Haemodorum*, arc the only native plant species in temperate south-eastern Australia possessing true bulbs. All three have large flowers, those of *C. flaccidum* being the largest of any native Victorian species (Willis 1970).

This paper introduces the biology of *Calostemma luteum, C. purpureum* and *Crinum flaccidum* at their temperate, southern limit on the River Murray floodplain in Victoria and South Australia. The main aims were to investigate germination and seedling behaviour and the way that growth, flowering and fruiting arc related to temperature and rainfall in naturally-occurring populations. As the conservation status of *Calostemma purpureum* and *Crinum flaccidum* is rare and vulnerable Victoria-wide respectively (Gullan, Cheal & Walsh

1990), we hope this paper will provide data useful for their management.

Species nomenclature follows Ross (1993) and Telford (1987).

DISTRIBUTION AND HABITAT

Crinum flaccidum occurs in all mainland states and reaches as far north as the Kimberley and inland from Townsville (Pate & Dixon 1982; Hewson 1987). North of the Murray River, *Calostemma* extends through New South Wales but only as far north as Rockhampton in Queensland (Telford 1987). Whilst *Calostemma* and *Crinum flaccidum* occupy river floodplains, swamps and other seasonally flooded sites (Pate & Dixon 1982; Telford 1987), *C. flaccidum* also occurs 'in the hills near Port Augusta' (Hannibal 1966) and *Calostemma* 'on sandstone hills and rocky rises' (Cunningham et al. 1981), indicating a capacity for non-flooded sites as well. Both genera can be found on soils ranging from deep sands (this study) to grey cracking clays (Moore 1984). They can be found

where flooding is short-lived, but not where water lies for long periods.

Crinum flaccidum may occur where mean annual rainfall is below 150 mm, such as in the Simpson Desert (Purdie 1984) and along the banks of the Clayton River north of Marree (Lothian 1957). In such areas, it is strictly confined to sites that receive supplementary moisture from runoff (F. J. Badman and P. K. Latz, personal communication). Less is known of *Calostemma* where it occurs in dry areas such as the Lake Eyre basin (Telford 1987).

The southernmost, temperate limit of *Crinum flaccidum* in Australia, the mouth of the Murray River at 35°30′S (Hewson 1987) is strikingly similar to the northernmost '*Crinum* Line', for *C. asiaticum* in Japan at 35°21′N (Koshimizu 1938) which coincides approximately with an annual mean temperature of 15°C and an annual mean minimum of −3.5°C (Koshimizu 1938). The corresponding Australian values (Victor Harbor data) are 16°C and 12°C.

Fig. 1. Distribution maps for (A) *Crinum flaccidum*, (B) *Calostemma luteum* and (C) *C. purpureum*, from Hewson (1987), Pate and Dixon (1982) and Telford (1987). Commonwealth of Australia copyright reproduced by permission.

Fig. 2. *Crinum flaccidum* plant about 400 mm high, margin of Lake Wallawalla, 1977.

In Victoria, *Calostemma and Crinum* are confined to the western part of the River Murray floodplain. The eastern limit of *Calostemma* is just downstream of the junction of the Murrumbidgee River with the Murray (Willis 1970, J. N. Macfarlane personal communication) (Fig. 3). By contrast, *Crinum* begins its range further west, just downstream of the junction of the River Darling with the Murray (Fig. 3). This may be related to *C. flaccidum* seed dispersal into the Murray by the waters of the Darling River (Zimmer 1946). The same may be true of *C. purpureum* and the Murrumbidgee.

In Victoria, *Calostemma* and *Crinum* occur on superficial sand ridges on the Murray floodplain except for a *Crinum* stand on clay at Lock 9 on the Murray River (Ashwell 1987). *Calostemma* and *Crinum* usually occur in treeless openings or woodlands of *Eucalyptus camaldulensis* and *E. largiflorens* (Ashwell 1987, Victoria: Department of Conservation and Natural Resources unpublished, this study, Table 1).

In *Calostemma*, we treated plants with large, wholly bright yellow flowers as *C. luteum* and all other flower colour forms as *C. purpureum* (see Telford 1987). These two taxa can occur in pure or mixed stands; they may be colour variants of a single species (Telford 1987). The abrupt change of colour forms downstream of the Murray–Darling junction (Fig. 3) could mean that the yellow plus purple and purple forms were dispersed to the Murray via the Murrumbidgee, whilst the pink and yellow forms (i.e. *C. luteum*) were dispersed to the Murray via the Darling. Dispersal only by water can mean that populations on separate river systems can become genetically isolated (Renner 1992).

At Wood's Lagoon, occasional *Calostemma* plants with white flowers can be found, whilst 8.2 km ESE of Ned's Corner Homestead at least six different *Calostemma* colour forms occur, including cream and white with pink stripes (F. E. Curtis, personal communication).

Sites for detailed study of the three species (Fig. 3, Table 1) were chosen to cover two flower colour forms of *Calostemma purpureum* and an attempt was made to include sites of differing recent rainfall history. When the work started, only a single stand of *C. luteum* (site 4) was known close enough to Melbourne for us to sample (Table 1). The Victorian stands (Fig. 3) were reported to us in May 1993 (F. E. Curtis, personal communication). The field work period was largely January to September 1992.

All sites chosen were on the Murray floodplain and all three taxa have dispersal units which can
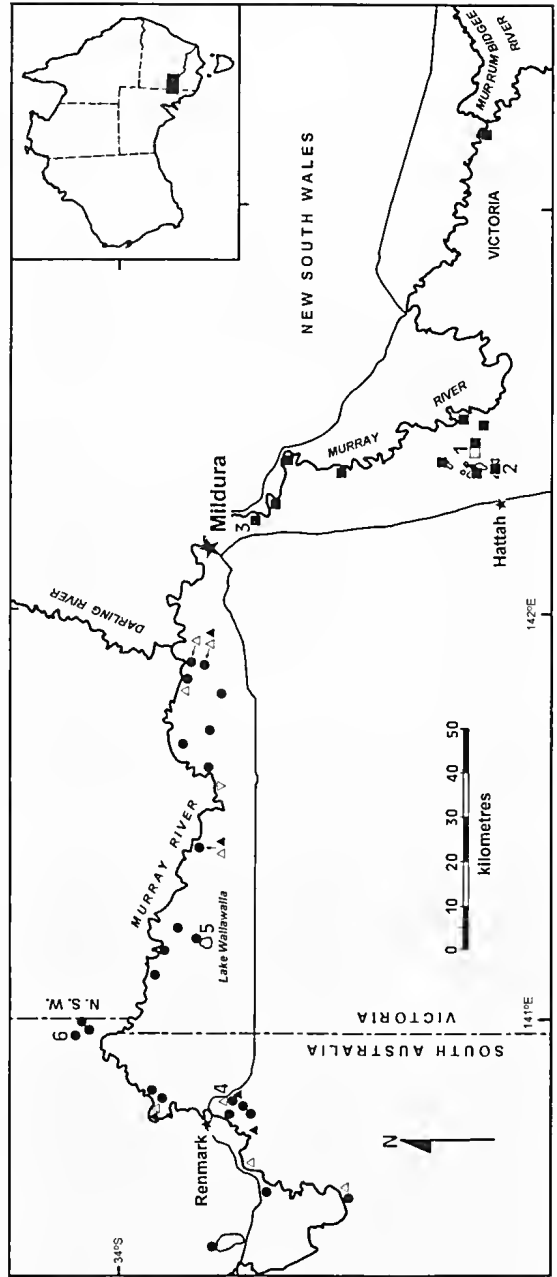
Fig. 3. Distribution of *Crinum flaccidum* (closed circles), *Calostemma luteum* (open triangles) and *C. purpureum* on part of the River Murray floodplain. For *C. purpureum*, open squares show stands with purple flowers and closed squares show stands with yellow flowers with purple markings; closed triangles show pink flowers. The open inverted triangle shows a *Calostemma* stand of unknown flower colour. The numbers show sites studied in detail.

Species	Site	Latitude, longitude	Surface soil texture	Habitat	Name of and distance to, nearest rainfall station
Calostemma purpureum (purple perianth)	1. Chalka Creek, Hattah Lakes area	34°43′17″S, 142°24′07″E	Loamy sand	Treeless opening just upslope from *Eucalyptus camaldulensis* woodland	Hattah–Kulkyne National Park Ranger's House, 7 km
C. purpureum (yellow and purple perianth)	2. Lake Bulla, Hattah Lakes area	34°45′30″S, 142°15′24″E	Loamy sand	*E. largiflorens* woodland	As above, 1.5 km
C. purpureum (yellow and purple perianth)	3. King's Billabong near Mildura	34°16′44″S, 142°14′34″E	Loamy sand	*E. largiflorens* woodland	Red Cliffs, 6 km
C. luteum (wholly bright yellow)	4. Paringa near Renmark	34°13′30″S, 140°48′32″E	Loamy sand	*E. largiflorens* woodland	Wonuarra Park homestead, 0.6 km
C. flaccidum	5. Lake Wallawalla, far NW Victoria	34°09′37″S, 141°11′30″E	Sand	Treeless sand ridge upslope from *E. largiflorens*	Ned's Corner homestead, 12 km
C. flaccidum	6. Gum Flat, Chowilla Station, E of Renmark	33°55′10″S, 140°57′19″E	Sand	Treeless sand ridge upslope from *E. largiflorens*	Chowilla homestead, 14 km

Table 1. General characteristics of the *Calostemma* and *Crinum* sites studied in detail.

float, so it is possible that distribution patterns may be related to floods. The six largest River Murray floods in the Mildura region (in order of decreasing magnitude) were in 1870, 1956, 1917, 1931, 1975, 1974 and 1981 (Victoria: Rural Water Commission 1986a). During the highest water levels since 1981 on 25–27 November 1992, none of the Victoria *Crinum* and *Calostemma* stands known to us was flooded. The floodwaters did not come close to any of the study sites (Table 1) except for site 5, where they were 10 m away in early December 1992.

Around Mildura and the Hattah Lakes, the *Calostemma* stands are elongate ones just above the 40 m contour, thus resembling a strandline. All were likely to be flooded for several months in 1956 (Victoria: Rural Water Commission 1986b), which would probably kill any submerged *Calostemma* plants. Major floods like those of 1956 and 1975 could deposit strandlines of *Calostemma* seeds, so producing linear stands along the flood margin which could subsequently colonize up- and downslope. Of course many present stands are likely to have resulted from the complex inter-action of a number of such colonizing events. Concentration of water-dispersed seeds at the land-water interface is well-known in other work (Schneider & Sharitz 1988).

Downstream of the Darling River junction, *Crinum flaccidum* can be found up to 12 km from the River Murray itself (e.g. at Boy Creek) Some, but not all, of the *C. flaccidum* sites flooded in 1956 (Victoria: Rural Water Commission 1986b, F. E. Curtis, personal communication). By con-trast, in this section, *Calostemma* stands are not found more than 4 km from the river itself and most or all of them flooded in 1956 (F. E. Curtis, personal communication).

It seems certain that some *Crinum* and *Calostemma* sites in South Australia near Renmark have not been flooded since 1870 or even earlier. Some stands, quite separate from the main ones at low altitudes, occur well upslope and seem certain to be above the level of even the largest flood imaginable, suggesting a seed dispersal agent other than water is operating. Seeds being carried and dropped by ravens or other birds is one possibility (D. Frahn personal, communication). In contrast, plants of the water-dispersed Central American *Crinum erubescens* only occur in strongly linear stands right at the land-water interface (Manasse 1990).

METHODS

Morphology and development of the dispersal units

Presence and maturity of dispersal units were

recorded approximately six weeks from 4 March 1992 to 7 September 1992 (hereafter called the sampling dates).

Morphology and development of bulbs and scapes

On the sampling dates, two to three bulbs were dug up at each site. Each was sectioned transversely one third of the way up the bulb from the base and the following recorded: depth of bulb (from soil surface to base of bulb), maximum bulb diameter, maximum leaf width, number of old scapes within bulb (present as dried remains), number of unemerged inflorescences within bulb and number of leaf bases found radially between each inflorescence.

Phenology

On the sampling dates, 50 marked plants at each site were scored for stage of flowering/fruiting, number of inflorescences, emerged leaf number and maximum leaf length. Using the methods of Orshan (1989) for any given date, the predominant phenomorphological state is presented; in practice, this meant that if less than 20% of plants exhibited a state, this was not recorded in the diagrams. Reproductive plants were scored as 'senescent' if the scape was still alive but all seeds had been dispersed or the scape had fallen.

Climate was monitored by rain gauges and maximum–minimum thermometers at the sites for the main study period from 4 March to 7 September 1992. Before and after this, values from the nearest meteorological stations had to be used (Table 1). Only the latter data are presented; the six-weekly rain gauge values were used as a check on their applicability. The seasonal temperature pattern was very similar right across the study area.

At site 4, an area 7 m × 5 m was hand-watered with 2250 L, 2250 L and 1000 L of water on 11, 18 and 26 February respectively.

Germination and emergence

Trials were conducted on the effects of temperature on germination and seedling development. All seeds were collected in March 1992. The temperature trial used seeds from sites 2 and 6 in the following regimes; (a) 25°C day/15°C night, (b) 15°C day/10°C night and (c) 2°C in constant dark. The photoperiod in (a) and (b) was 14 h. All seeds were placed on damp, sterile sand in covered transparent dishes replicated five times, 20 seeds per replicate for Calostemma, 12 for Crinum. The 2°C treatment

was chosen to see if the taxa behaved like tropical taxa with recalcitrant seeds at low temperatures.

Responses of seeds and seedlings to burial and watering

This trial used seeds from sites 1, 2 and 6. It was designed to see if burial or watering has important effects on germination or seedling development, the watering because all taxa can germinate and grow for some time without added water.

There were two watering regimes (watered regularly and unwatered) × two burial regimes (buried and unburied) × four replicates. The buried seeds were covered by 0.5 to 1 times the seed diameter of sand and the watered treatments used drained containers. Each replicate consisted of 20 seeds in plastic containers 20 × 26 × 8.5 cm filled with sterile river sand. The trial ran in an unheated glasshouse for three months starting on 13 March 1992. Presence and length of cotyledon, leaf and root were recorded every 14 days.

The term germination will be used here to mean the emergence of the radicle and part of the cotyledon from the seed (Fig. 4). Two subsequent events studied as well were root emergence, the emergence of an adventitious root from the cotyledon just behind the radicle and leaf emergence, the emergence of the first foliage leaf through the side of the cotyledon slightly further back (see Rees
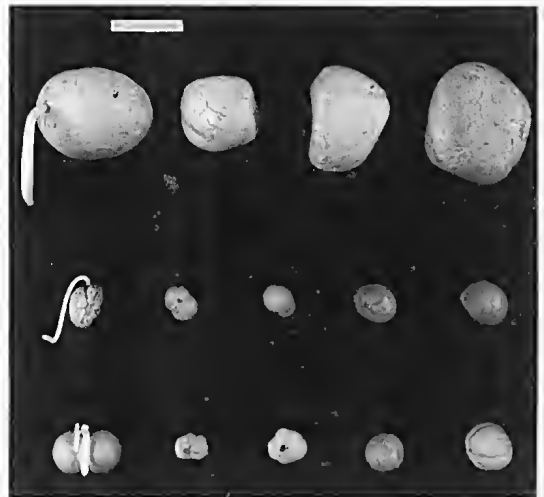
Fig. 4. Dispersal units of *Crinum flaccidum* (top row), *Calostemma purpureum* (middle row) and *C. luteum* (bottom row). The left hand units have already germinated without an external water supply. All units from site 4. Scale bar = 20 mm.
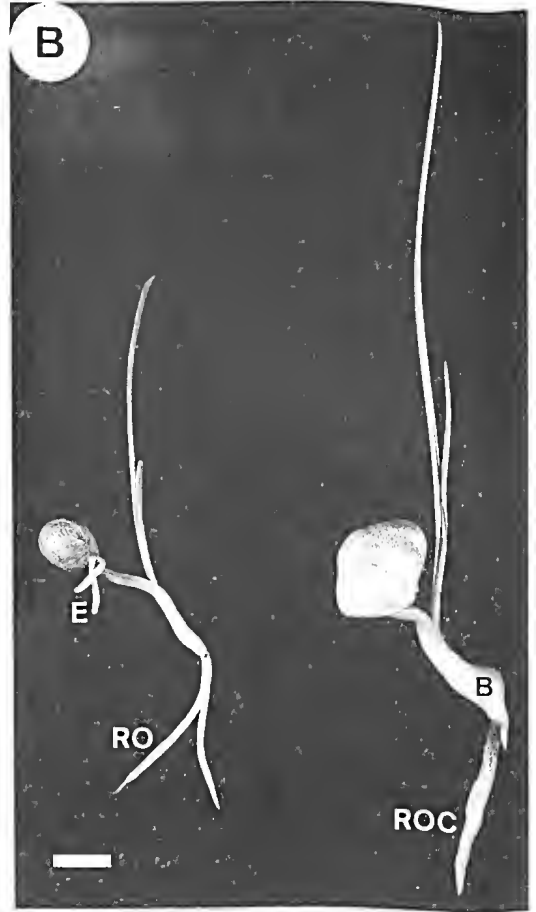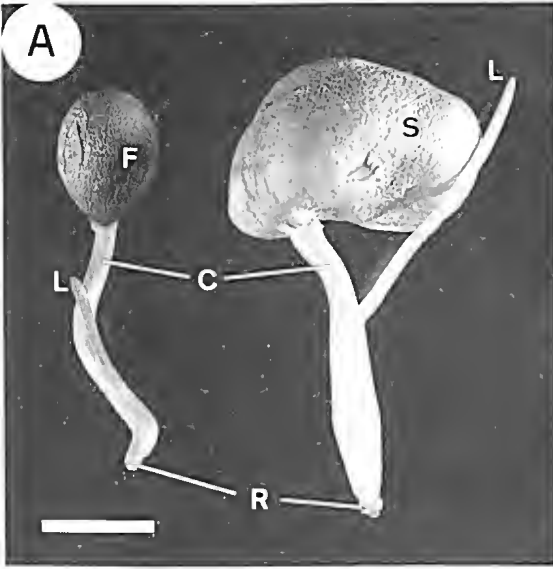
Fig. 5. A, B, seedlings of *Calostemma purpureum* (left) from Lambert Island and *Crinum flaccidum* (right) from Paringa showing bulb (B), cotyledon (C), young embryos (E), fruit (F), first leaf (L), radicle (R), root (RO), contractile root (ROC) and seed (S). A, seedlings four weeks old. B, same seedlings seven weeks old. Scale bar = 10 mm.
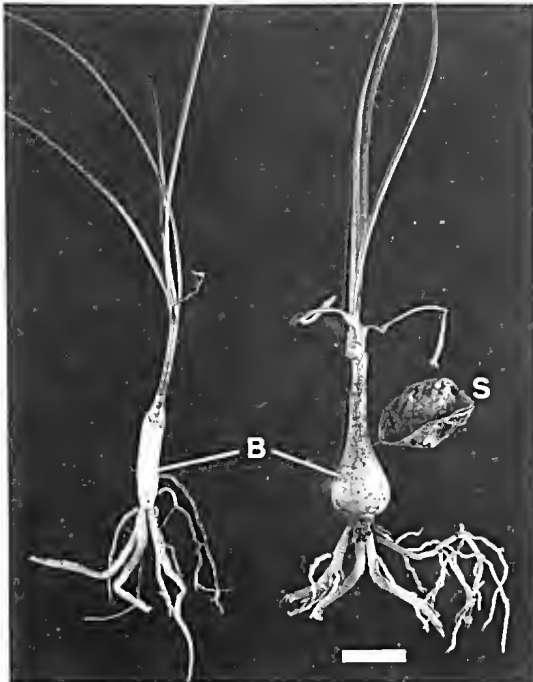
1972; Pate & Dixon 1982; Figs 5 and 6). These two events are seemingly independent — they do not occur in a fixed order.

Effects of seed storage

Four seeds of *Crinum* (site 5) and 11 seeds of *Calostemma* (site 3) were stored dry at 4°C for 2 months (by which time they had germinated). They were then stored dry for a further 21 months in the dark at room temperature and examined for viability.

Fig. 6. Plants of *Calostemma purpureum* (left) from site 2 seed source and *Crinum flaccidum* (right) from site 5 seed source. Plants were grown from seed in pots for 13 months. Showing bulbs (B) and remains of seed, now detached (S). Scale bar = 20 mm.

Buoyancy of the dispersal units

Ungerminated seeds of *Calostemma* (sites 1 and 2) and newly-germinated seedlings of *Crinum* (site 6) were available. These were added to containers (20 cm × 26 cm × 8.5 cm) containing either tap-water or seawater. The sea water treatment was included because many species of *Crinum* are coastal and thought to be dispersed by ocean currents (Koshimizu 1930; Hannibal 1966) and because Hannibal (1966) suggests that *C. flaccidum* may have arisen as a coastal species in the Gulf of Carpentaria. There were four replicates, with 20 (*Crinum*) or 25 (*Calostemma*) seeds per replicate. Every two weeks, the water was changed and sunken or rotted seeds or seedlings recorded. The rotted ones were removed. The trial ran in an unheated glasshouse for two months (mid-March to mid-May).

RESULTS AND DISCUSSION

Morphology and development of the dispersal units

At site 4, *Calostemma luteum* and *C. purpureum* plants in full flower on 12 April 1993 had mature seeds as few as three weeks later; for *Crinum* there the corresponding figure was 5.5 weeks (D. Frahn, personal communication). For the South African *Crinum bulbispermum*, seeds can mature two to three weeks from flowering (Oliver 1990) and for *C. erubescens* the figure is 45 days (Manasse 1990).

Crinum flaccidum produces large seeds up to 25 mm in diameter, weighing up to 11 g (mean weight 5 g) and with a high water content of 89% (Fig. 4; Howell 1984; Howell & Prakash 1990). Seeds up to 66 g in weight are known in *C. erubescens* (Manasse 1990). Vivipary — germination while the seed is still attached to the parent plant — is rare; normally it occurs 2–4 weeks from seed shed. No external water supply is required for this (Howell & Prakash 1990).

Less is known of *Calostemma*. The organ that is shed from the parent plant is a capsule. This is normally one-'seeded'. However, it is likely that the 'seeds' are, strictly speaking, bulbils (Telford 1987). For brevity, the dispersal units of both *Crinum* and *Calostemma* will often be referred to below as seeds.

Calostemma germination normally occurs within a few weeks after seed shed as one to three embryos extrude through the fruit wall. Again no external water supply is required. No dispersal unit differences were noted between the two species of *Calostemma*, with diameters of 5 to 12 mm, mean weights of 0.6 g and high water contents.

A group of genera in the Amaryllidaceae has large, soft dispersal units of high water content (60–90%) which lack dormancy and are often viviparous. It includes *Amaryllis, Brunsvigia, Crinum, Haemanthus,* and some other South African genera (Isaac & McGillivray 1965; le Maitre & Midgley 1992). Clearly, *Calostemma* should be added to this group. Such dispersal units, called 'water-rich seeds' by Dahlgren, Clifford & Yeo (1985), are similar to many recalcitrant seeds in their large size, high water content and lack of dormancy. Presumably, like non-dormant recalcitrant seeds, they are imbibed when shed and so germinate then or soon after, as is the case for *Avicennia marina* (Verbenaceae) and *Sechium edule* (Cucurbitaceae). In these cases the young seedling can then survive for months prior to either establishment or receipt of external water supplies (Chin 1988; Newstrom 1989).

Morphology and development of bulbs and scapes

Crinum. The largest bulb seen was 146 mm across and contained the remains of 8 old scapes, 7 unemerged inflorescences and about 60 leaf bases in keeping with a genus noted for its enormous bulbs (Hitchmough 1989). Bulbs smaller than 45 mm across had never flowered and did not contain unemerged inflorescences. The latter were present in bulbs larger than 45 mm at all sample dates.

The *Crinum flaccidum* bulb appears to be made up entirely of leaf bases; nothing was recognizable as scales, so that the bulb is the *Hippeastrum* type (Rees 1972). In *C. flaccidum*, the usual number of leaf bases between inflorescences is five, with a range from three to seven.

Inflorescences are initiated in the centre of the bulb and move outwards as newer leaf and floral buds are formed (Fig. 7). At flowering, there are generally three unemerged inflorescences within the bulb, with the oldest inflorescence, furthest from the centre, being the emergent one. Thus the bulb has a sympodial branching system like *Hippeastrum* (Rees 1972) rather than the monopodial system suggested for *C. flaccidum* by Howell & Prakash (1990).

The fact that unemerged inflorescences at all stages of development separated by about five leaf bases were found at all sampling dates indicates that bulb growth and inflorescence initiation are more-or-less continuous processes, at least while emerged leaves are present. In the absence of seasonal trends, the bulb data from different sampling dates were pooled (Table 2).

Regarding the depth to which the bulbs are buried, Pate and Dixon (1982) recorded 500 mm for *Crinum asiaticum* and regarded it as 'a remarkably great depth for a bulbous species'. However, for *C. flaccidum*, we recorded 600 mm, while 900 mm (Lothian 1969) and even 1200 mm (D. Frahn, personal communication) have also been recorded.

Calostemma. No important differences were found between populations (Table 2). The largest

bulb was 56 mm across. The two smallest bulbs, 15 mm across, had never flowered but the two next-smallest ones, 18 mm across, had flowered as had nearly all the others.

By the first sampling date, the 1992 inflorescences had already emerged. In all flowering bulbs seen, three inflorescences had been initiated in the months prior to the most recent flowering, all between the same two leaf bases and at slightly different ages (Fig. 8). In the bulb sections, the remains of old scapes could again be seen. Remains
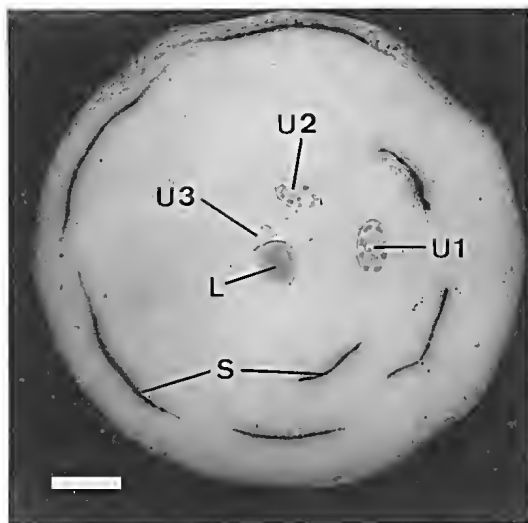
Fig. 7. Transverse section of *Crinum flaccidum* bulb collected at site 6 in June 1992 showing young unemerged leaves (L), remains of old scapes (S) and first, second and third unemerged inflorescences (U1, U2, U3). Scale bar = 20 mm.
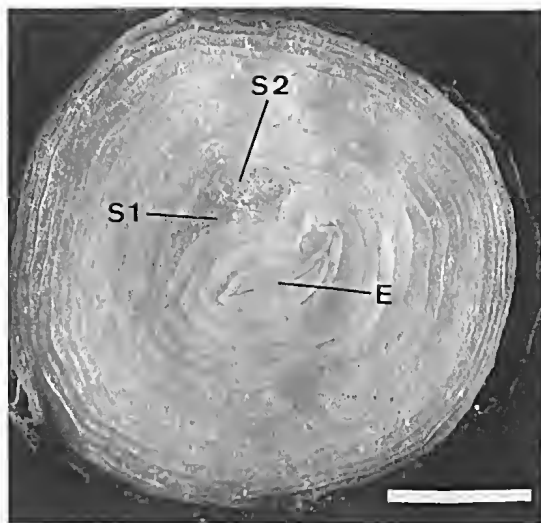
Fig. 8. Transverse section of *Calostemma purpureum* bulb collected at site 3 on 17 May 1993 showing bases of emergent leaves (E) and two of the three scapes from the current season's flowering (S1 and S2). Scale bar = 10 mm.

Species	Site	Depth of bulb (mm) Mean	Depth of bulb (mm) Range	Bulb diameter (mm) Mean	Bulb diameter (mm) Range	Number of old scapes in bulb[1] Mean[2]	Number of old scapes in bulb[1] Range[2]	Number of unemerged inflorescences in bulb Mean[2]	Number of unemerged inflorescences in bulb Range	Mean number of leaf bases between inflorescences[3] Mean	Mean number of leaf bases between inflorescences[3] Range
Crinum flaccidum	5	246	150–358	68	18–116	4	1–7	4	1–6	5	3–7
C. flaccidum	6	303	195–600	85	47–146	4	1–8	4	1–7	5	4–7
Calostemma luteum	4	115	75–190	38	21–51	3	2–5	—	—	6	5–7
C. purpureum	1	129	85–195	36	18–47	2	1–4	—	—	7	5–9
C. purpureum	2	233	95–320	43	15–56	3	1–5	—	—	7	5–12
C. purpureum	3	139	85–205	34	15–50	3	2–4	—	—	7	5–9

Table 2. Bulb characteristics for *Crinum flaccidum*, *Calostemma luteum* and *C. purpureum*, combined over six sampling dates from March until September 1992. [1]For *Calostemma*, these numbers are the groups of three inflorescences formed each flowering season. [2]These values do not include bulbs which have never initiated inflorescences. [3]These are population means obtained by averaging bulb means. For *Calostemma*, they are the numbers of bases between groups of inflorescences from a single flowering season.

of groups of three inflorescences from up to five past flowering seasons were found.

At all sites in April–June, some bulbs contained the dead, dried remains of unemerged inflorescences; these are described here as being aborted (see phenology section). If less than three inflorescences emerge in a season, the remainder abort. Such abortion was never seen in *Crinum flaccidum*.

Unlike *Crinum*, no live unemerged inflorescences were found at any time from March to September, suggesting flower initiation no more than once a year rather than the more continuous *Crinum flaccidum* pattern. In the bulbs sampled on 7 September 1992, there was no sign of flower bud initiation in advance of the next summer's flowering; this presumably must occur some time in the September–January period given the normal flowering time. If flower bud initiation was not until summer, this could explain why spring to early summer rains do not produce flowering, whereas late summer rains do (see later). In *Calostemma*, leaf growth occurs between flowering periods, typically producing six to seven leaves. Unlike *C. flaccidum*, *Calostemma* inflorescences emerge from amongst the leaf rosette.

In *Crinum*, it takes from four to five years from germination to flowering (Hitchmough 1989), whilst for *Calostemma* it takes about three years (J. Belling, personal communication).

Maximum bulb depth recorded in *Calostemma* was 320 mm (Table 2).

Crinum flaccidum and *Calostemma* are often found in groups, clumps or colonies. In other bulbous geophytes, such behaviour has been related variously to bulb division and to restricted seed dispersal (see e.g. Nault & Gagnon 1993). These factors are considered here in turn.

Production of daughter bulbs by bulb division was found rarely (1 out of 41 bulbs for *Crinum*, 7 out of 72 for *Calostemma*). The daughter bulbs arise from lateral buds between the leaf bases. They are also produced occasionally by *Crinum asiaticum* (Pate & Dixon 1982) and prolifically by some African Crinums (Verdoorn 1973).

During fruit development of *Crinum flaccidum* and *Calostemma* the scape lengthens and bends under the weight of the fruit so that the attached fruits eventually come to lie on the soil surface. Groups of the large, heavy seeds can be found germinating exactly where they were deposited by the bent-over scapes. Given the rarity of bulb division, such restricted seed dispersal may be the main cause of clumping. Especially in *C. flaccidum*, two clumps can often be found approximately the same distance apart as the mature scape length, possibly representing offspring clumps. Similar behaviour

has been suggested in the amaryllid *Haemanthus* (Snijman 1984) and other monocot geophytes (Bierzychudek 1982) as well as in *Plantago lanceolata* and some other dicots (Gilbert 1989). Clumping can also be caused by bulb division (see e.g. Barkham 1992; Nault & Gagnon 1993) and mass germination from mice seed caches (Nault & Gagnon 1993).

In *Haemanthus*, with similar large, soft seeds to *Crinum* and *Calostemma*, there is little evidence that animals eat or disperse the seeds; these are probably too soft to survive passage through animal digestive tracts (Snijman 1984). The only animals recorded eating *Crinum flaccidum* or *Calostemma* seeds are emus, seen eating large quantities of *Calostemma* seeds at Hattah Lakes on a number of occasions (J. H. Browne, personal communication). Their faeces did not contain any intact *Calostemma* seeds, making dispersal by emus seem unlikely.

Phenology

The main aim of the account below is to examine the extent to which rainfall and temperature influence leaf and flower emergence.

Crinum. At site 5 on 4 March 1992, only 10% of plants had any live, emergent leaves and only 8% of plants were reproductive (mostly in fruit). This followed a very dry summer, with only four light showers; 0.6 mm in December, 3 mm in January and 3 mm on both 4 and 5 February. After 27 mm of rain in late March–April, 69% of plants had emergent leaves on 5 May and this reached a maximum of 90% by 16 June after further rain. However no further plants flowered additional to those which were reproductive on 4 March (Fig. 9).

The nearest rainfall station to site 6, 14 km away (Table 1), had similar rainfalls to site 5, with none in December–January and only 5 mm in February, on the 6th. We presume that site 6 itself received more rain than this because by 4 March, 75% of plants had emergent leaves and 42% were reproductive (nearly all in fruit). With no further rain, these active plants had died back by 28 March. As at site 5, April rains then produced widespread leaf emergence but no further flowering (Fig. 9).

The whole area received very high rainfall from September through to January 1993. Near Renmark, some flowers had appeared by mid-December 1992, with peak flowering in about mid-February 1993. Occasional flowers of *Crinum* can be found on a variety of dates, e.g. June and September 1992 (D. Frahn, personal communication).
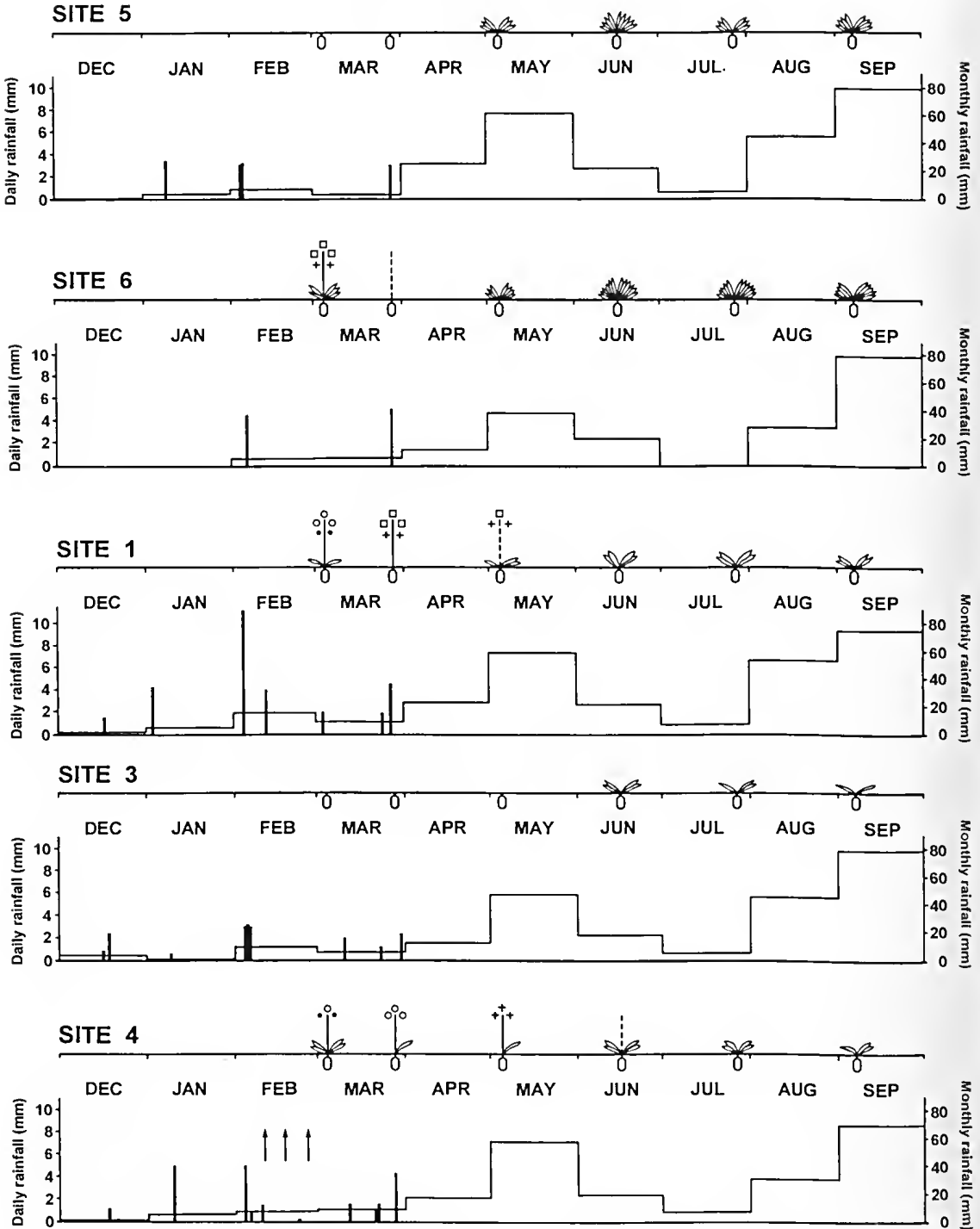
Fig. 9. Rainfall and phenology of *Crinum flaccidum* (sites 5 and 6), *Calostemma luteum* (site 4) and *Calostemma purpureum* (sites 1 and 3). Closed circles = buds, open circles = flowers, squares = fruits, crosses = seed dispersal, dashed lines = dead or senescent scapes. In the rosettes, mean leaf number is shown. Narrow, filled bars are daily rainfall (December 1991 to March 1992 only); wide, unshaded bars are monthly rainfall. For site 4, the arrows are the three irrigation events and the data shown are from the irrigated plot.

Leaf number per plant was highly variable, with up to 36 being recorded.

Our findings agree with earlier work that *C. flaccidum* generally has a summer–autumn flowering time in southern Australia (see Cunningham et al. 1981), with no flowers being found after May (see Howell 1984). In our sites, rains after March produced leaf emergence but no flower emergence.

In January–February–March, even light showers like 6 mm as at site 5 can produce some flowering (8% of plants; not shown in Fig. 9). As a result, the species flowers virtually every year in our study area (D. Frahn, personal communication). In the drier climate of Central Australia, flowers are usually seen only every two to three years (P. K. Latz, personal communication). The flowering response is very rapid. For example, 30 mm of rain on 28 February 1987 at Paringa was followed by a mass flowering event two weeks later (D. Frahn, personal communication). North of our area, earlier flowering can occur, e.g. November at Kinchega (T. Auld, personal communication) and June–July near Marree in northern South Australia (Lothian 1957).

Despite the view that *C. flaccidum* leaves die back in winter (Howell 1984), we found maximum leaf length then (see Cunningham et al. 1981) and dying back of leaves seemed more related to declining soil water supply. In *C. flaccidum*, only very young leaves showed intact leaf tips; the rest have lost their tips in such a way that they seem to have been cut off along a line straight across the leaf blade. In South African Crinums, this is due to the leaves dying back to the base in winter and growing out again later (Verdoorn 1973). For *C. flaccidum*, low soil water supply seems the most likely cause. After good rains, *C. flaccidum* leaves over 1 m in length are common, up to 1.5 m (D. Frahn, personal communication).

The genus *Crinum* is regarded as basically tropical and sub-tropical, generally showing summer growth in summer rainfall climates (Hitchmough 1989). *C. flaccidum* has been treated as an exception to this, and regarded as a 'winter rainfall species' (Hitchmough 1989). However, in northern Australia *C. flaccidum* is dormant during winter, which is the dry season (Pate & Dixon 1982), so it may be more accurate to regard *C. flaccidum* as an adaptable species which grows whenever water is available.

Calostemma. Sites 1 and 2 results were similar so only the site 1 data are given. At site 1, there was only 1 mm of rain in December and 4 mm in January. However, following 11 mm on 4–5 February and 4 mm on the 12th, by 4 March 78% of plants had small emerged leaves and 74% were reproductive. After a dry March, most leaves died. Leaves, but not flowers re-appeared after April rains (Fig. 9). All plants remained in leaf but without flowers throughout winter.

Site 3 also had a very dry December–January, but only 9 mm of rain in February, spread over the 4th, 5th and 6th. On 4 March no plants were reproductive or had emerged live leaves; plants could only be found with difficulty. They remained like this through a March–April dry period and finally produced leaves after rains in May (Fig. 9). None became reproductive in 1992.

At site 4, February was even drier than site 3, with a total of only 7 mm from showers of 5, 1 and 1 mm on the 4th, 6th and 10th. As at site 3, no non-irrigated plants flowered in 1992. The irrigated plants all produced leaves by 4 March, and nearly all had flower buds or flowers. As at site 1, many leaves died back in the March dry period. Further leaves appeared after rains in May, but no further flowers (Fig. 9).

At sites 3 and 4 but not at sites 1 and 2, the unemerged inflorescences had aborted by 5 May, correlated with drier March–April conditions at the former two sites. Such abortion was not seen at sites 1 and 2 until 16 June, following good rains in May–June. It is likely that water deficit caused abortion at sites 3 and 4, but this is most unlikely at sites 1 and 2 where the cause may be related to frosts, low temperature or some other factor.

Despite the high rainfalls no flowers were seen at any *Calostemma* site from September to December 1992. In our area, flowers can be found in January but not in December. This also applies to *Crinum flaccidum* (our observations; F. E. Curtis, personal communication). Peak flowering occurred in early February 1993 both at site 3 and site 4 (J. H. Browne & D. Frahn, personal communication).

Our data agree with earlier suggestions of a summer–autumn (Cunningham et al. 1981) or January–April (Elliot & Jones 1982) flowering time for both species. As for *Crinum*, rains after March produced leaf emergence but no flower emergence.

In our study, a fall of rain of 15 mm in summer was enough to produce flowering, while 4 mm (site 4) and 9 mm (site 3) were not. Accordingly, *Calostemma* flowers much less frequently than *Crinum*; for example, at Kinchega National Park, with a mean annual rainfall of 236 mm, *Calostemma* has not been seen flowering since March 1987, while *Crinum flaccidum* has flowered several times at least (T. D. Auld, personal communication, 1992).

The most important trigger for growth in herbaceous perennials in the Mojave Desert is a fall

of rain of 25 mm or more in autumn and called by Beatley (1974) the critical rainfall event. For growth of herbaceous monocots in Perth, Western Australia, the critical rainfall event is greater than 17 mm in autumn (Bell & Stephens 1984). This is similar to the value for *Calostemma* shown here, whereas for large-bulbed species like *Crinum flaccidum* we believe that the value is significantly less.

Calostemma leaf growth continued throughout winter, confirming earlier views that *Calostemma* species show predominantly cool-season leaf growth (Cunningham et al. 1981; Hitchmough 1989). The leaves then decline in late spring (Hitchmough 1989). It is not known to what extent this is simply a reflection of declining soil moisture supply.

In our area, *Calostemma* plants are normally dormant in early summer until both leaves and scapes start growing after rain. In plants which are going to flower, the leaves usually produce 20 mm or so of green tissue and then stop, at the stage where they are either slightly emergent or not quite emergent. Leaf growth then resumes later once fruiting is over. This behaviour is probably why *Calostemma* is said to have 'leaves developing mainly after flowering' while *Crinum flaccidum* is said to have 'leaves well-developed during flowering' (Jessop 1981).

General discussion.   Regarding geophyte life cycle types, the Amaryllidaceae is one of the main families in which many species in South Africa and the Mediterranean show hysteranthous behaviour (Dafni, Shmida & Avishai 1981), namely the flowers and leaves appear at separate times of the year, the flowers in early autumn before rain has fallen to break the summer drought, and the leaves a month or so later with the first rains (Dafni, Cohen & Noy-Meir 1981). In Israel, all autumn-flowering geophytes are hysteranthous (Dafni, Shmida & Avishai 1981). Although *Calostemma* (and *Crinum*) can flower in autumn (and summer), they show some leaf growth at flowering and do not flower in the absence of rain, so are not hysteranthous in the sense of Dafni, Cohen & Noy-Meir (1981). Hysteranthy is seen as an adaptation to declining rainfalls (le Maitre & Midgley 1992).

The flowering behaviour of *Crinum flaccidum* and *Calostemma* contrasts strongly with the predominantly spring flowering of the geophytes introduced to southern Australia from Europe and South Africa (see e.g. Parsons & Cuthbertson 1992). While the geophytes of southern Africa mostly flower in spring (Pierce & Cowling 1984), those in the Amaryllidaceae mostly flower in autumn, presumably because the lack of seed dormancy in those with fleshy seeds restricts flowering and seed dispersal to the period shortly before the winter rains (Johnson 1993). The present data accord with this in general, although the flowering times are somewhat earlier than typical for taxa with fleshy seeds. Similarly, the bulbous Amaryllidaceae of the Sonoran Desert only produce leaves and flowers following summer rains, while some bulbous Liliaceae there are only active after winter rains (Shreve & Wiggins 1964). For *Crinum* and *Calostemma* in our area, at least some summer rain seems to be important for flowering to occur. It is not known if there are temperate areas where lack of such rainfall excludes them.

For the species studied here, growing in highly variable rainfall and flood regimes, relatively wet conditions allow both vegetative and reproductive development to occur, as at sites 1, 2 and 6, whilst drier conditions allow only vegetative development (e.g. sites 3 and 4). Given the extension of all three species into far drier areas than the study area, we assume that in drought conditions the bulbs can remain totally dormant for at least a year and probably for much longer (see also Evenari, Shanan & Tadmor 1971; Boeken & Gutterman 1989).

Germination and emergence

In the temperature trial, germination and leaf and root emergence were reduced at 2°C. Final percentages for all three processes were higher for *Calostemma* than *Crinum* at 15°C, while the reverse was true at 25°C (Table 3). This is consistent with the fact that *Calostemma* has a more temperate range, being restricted to areas south of the Tropic of Capricorn whilst *Crinum flaccidum* extends up to 18°S (Hewson 1987; Telford 1987). Germination

Temperature	2°C	15°C	25°C
Germination (%)	.		
Crinum	58	75	83
Calostemma	37	100	75
Leaf emergence (%)			
Crinum	10	45	70
Calostemma	0	77	53
Root emergence (%)			
Crinum	0	67	77
Calostemma	0	77	53

Table 3. Germination, leaf emergence and root emergence for *Calostemma* (site 2) and *Crinum* (site 6) after 68 days at three temperature regimes.

and seedling survival were surprisingly high at 2°C. In this, the populations behaved similarly to temperate taxa with recalcitrant seeds like some *Quercus* sp. rather than to most tropical taxa with recalcitrant seeds (Chin 1988).

Responses of seeds and seedlings to burial and watering

No effects of watering or burial on germination were found, but in the watered, buried treatment 24% of *Crinum* and 6% of *Calostemma* seedlings were killed by rotting of the cotyledon and seed as occurs in *Crinum erubescens* (Manasse 1990). In all treatments, every seed which germinated subsequently produced a foliage leaf. However rate of leaf growth and final leaf length was small in the unwatered treatments, bigger in the unburied watered treatment and bigger still in the buried watered one (Fig. 10). Root emergence occurred in all the watered seeds but not the unwatered ones; seed burial did not have significant effects on this. All three taxa showed similar treatment response (Fig. 10).

At the end of the trial, all taxa had produced more swelling in the area where the bulb forms in unwatered than watered treatments, suggesting that growth is somehow flexibly partitioned between either bulbs or roots depending on water regime. Maximum bulb size was 2.5 cm in diameter (in *Crinum*). Final leaf number was two to three. For *Crinum,* final root number was two, of which the oldest had a transversely enfolded surface and so was probably contractile.

Effects of seed storage

In the long-term dry seed storage trial, all seeds had germinated by 2 months. At 23 months, all *Calostemma* seedlings were desiccated, shrunken and dead. Most had produced the first, and some the second, leaf before dying. Some swelling in the bulb region occurred. However, half the *Crinum* seedlings were still alive, having produced two to three leaves of which the most recent on each plant was still alive. Bulbs were up to 15 mm diameter and still contained moist, white tissue, although they had begun to shrink. The seeds were totally desiccated and shrunken as before. In both taxa, roots had not developed beyond a tiny protrusion. However, the surviving *Crinum* seedlings, when planted in moist soil, rapidly produced healthy, normal roots. The longer survival time of *Crinum* than *Calostemma* seedlings is probably related to the much larger seed size of the former. For *Crinum asiaticum* seeds after two years in a desiccator, 62%

were still alive (made up of 28% seedlings and 34% ungerminated seeds) (Koshimizu 1930).

The positive geotropism of the elongating cotyledon means that the shoot apex can become buried, so that cryptogeal germination can occur as described for other Amaryllidaceae. This is thought to be an adaptation which protects shoot apices from drought or fire (Fahn & Cutler 1992). Whilst this can occur in *Calostemma* and *Crinum* without an external supply of water, our results suggest that further shoot burial due to root contraction cannot, as root growth was negligible in dry soil. The maximum extent to which the cotyledon can elongate is about 70 mm in *Crinum* and 50 mm in *Calostemma*. A preliminary trial placing seeds on dry coarse sand showed that in some cases the cotyledon elongates without burying the shoot apex while in others the shoot apex can be buried to maximum depths of 18 mm (*Crinum*) or 17 mm (*Calostemma purpureum*) after 2.5 months.

Buoyancy of the dispersal units

All *Calostemma* seeds germinated during the trial, so that, for all populations, treatment effects were on seedlings.

Nearly all *Crinum* seedlings remained alive throughout the trial (Table 4). Those in seawater showed little new growth. In fresh water, growth was faster, with all developing roots and leaves. Buoyancy remained high and after 62 days ranged from 86% in fresh water to 92% in seawater.

In *Calostemma*, in strong contrast to *Crinum*, most seedlings were killed by seawater and rotted, with final viable seedling percentages of 14 and 1 for the two populations (Table 4). None of these viable seedlings was still floating. All seedlings in fresh water remained viable, with buoyancies at 62 days of 56% (site 1) and 83% (site 2).

The data from fresh water strongly suggest that both *Crinum* and *Calostemma* are capable of water-borne dispersal in rivers and streams. In *Crinum flaccidum* and other Crinums, seed buoyancy is thought to be related to corky layers in the endosperm (Howell & Prakash 1990). For those Amaryllidaceae with large, soft, fleshy seeds, seed buoyancy may be a common corollary of their seed morphology. For example, water-borne seed dispersal has been suggested for most species of *Haemanthus* (Snijman 1984). In *Crinum erubescens*, seeds only sink if they are inviable (Manasse 1990).

While the salt water treatment did not adequately simulate wave action, ocean temperatures or risk of damage by marine organisms, the present buoyancy and viability data certainly make dis-
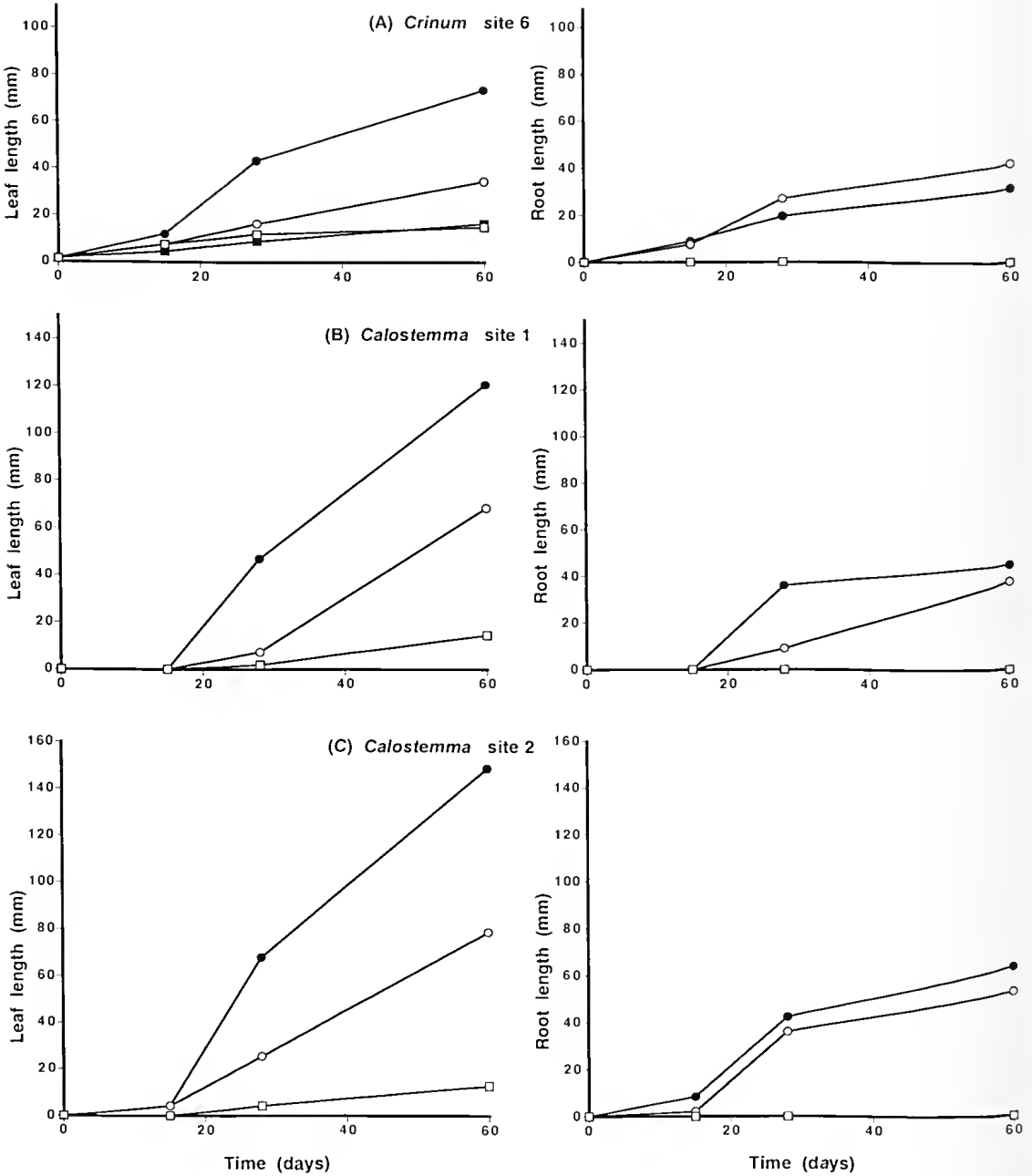
Fig. 10. Leaf and root growth for seedlings of *Crinum flaccidum* and two populations of *Calostemma purpureum* in four treatments; watered, buried (closed circles); watered, unburied (open circles); unwatered, buried (closed squares); unwatered, unburied (open squares). Closed squares not shown when coincident with open squares.

Species		Time (days)			
		22	35	49	62
Crinum	Seawater	100	100	100	95
flaccidum	Fresh water	100	100	100	100
Calostemma					
purpureum					
Site 1	Seawater	100	1	1	1
	Fresh water	100	100	100	100
Site 2	Seawater	100	26	14	14
	Fresh water	100	100	100	100

Table 4. Viability (%) of dispersal units of *Calostemma purpureum* and *Crinum flaccidum* in seawater and fresh water. N = 80 for *Crinum* and 100 for *Calostemma*.

persal via ocean currents a possibility for *Crinum flaccidum*. Similar trials show that seedlings of the coastal *C. asiaticum* can float and remain viable for more than two years (Koshimizu 1930) and seeds and seedlings of both it and *C. americanum* are said to float in seawater for at least a month and to be washed up live on beaches (Gunn & Dennis 1976). Thus the behaviour of *C. flaccidum* in seawater echoes that of other members of the genus, even though its present distribution is explicable without invoking dispersal by ocean currents. The majority of plant dispersal units are thought not to float in either fresh water or seawater (Gunn & Dennis 1976).

Calostemma purpureum dispersal units are clearly much less able both to float and to remain viable in seawater than those of *Crinum flaccidum*, not surprisingly in a genus with no known coastal connections.

CONSERVATION

It is hard to assess the conservation status of these taxa. In Victoria, the Mallee Survey of 1985–86 sampled five stands of *Calostemma* and seven of *Crinum* on public land (Cheal & Parkes 1989 and personal communication). There are other public land stands as well and probably at least half the public land stands are in biological reserves. Low palatability to grazing mammals is also in favour of these taxa (Cunningham et al. 1981). Sheep and/or rabbit grazing damage has been seen on *Calostemma* leaves at times but not on those of *Crinum* (F. E. Curtis, personal communication). It has been reported to us that wild pigs dig up and eat *Crinum flaccidum* bulbs over big areas on Lindsay Island (J. Hart, personal communication). Work is needed on this, on the extent of seed

predation by emus (as seen at Hattah–Kulkyne National Park) and on whether there is an effect of changing flood regimes on the ecology of these taxa before we understand whether there are significant threats to them. Our sites would not have been flooded since 1981 and probably earlier. From the wide range of plant sizes present (including bulb diameters), we assume that flooding is not necessary for recruitment.

The low palatability of *Crinum* and *Calostemma* is not surprising given the widespread development of poisonous alkaloids in geophytes including those in the Amaryllidaceae (Tomlinson 1980; Dahlgren et al. 1985).

After a paddock containing *Crinum flaccidum* was ploughed in the Paringa area, the adult *C. flaccidum* plants survived by resprouting from the bulbs (D. Frahn, personal communication).

CONCLUDING DISCUSSION

When the main seasonal stress is drought, the stored water and carbohydrate found as part of the bulbous habit allow the plant to survive prolonged drought and then to sprout as soon as rain falls in *Calostemma* and *Crinum flaccidum*. Flowering can occur as little as two days after heavy rain in *Habranthus* (Solbrig & Simpson 1977). Possession of a bulb both gives the plant temporary independence from an external water supply and allows preformation of flower buds within the protection of a storage organ (Burtt 1970). Such preformation (found in both *Calostemma* and *Crinum*), in turn allows plants to respond immediately to favourable growing conditions and to complete their life cycles quickly (Caldwell 1969), the rain merely serving as a trigger for final development of the inflorescence (Danin 1983). The bulb also facilitates partial or complete uncoupling of the leafing and flowering phenophases (Johnson 1993).

Apart from behaviour related to their bulbs, *Calostemma* and *Crinum flaccidum* also share with many other Amaryllidaceae the possession of large, buoyant, non-dormant, water-rich seeds. These characteristics have important implications for seed dispersal (see above). The effects of non-dormancy of seeds on seedling establishment are not well-understood. It has been suggested that seed non-dormancy is a strategy allowing seedlings of *Crinum flaccidum* to become established either before winter frosts (Howell 1984) or at a time when other species are competitively disadvantaged (Howell & Prakash 1990). Further work is needed before this issue will be understood.

ACKNOWLEDGEMENTS

REFERENCES

ASHWELL, D., 1987. Floodplain vegetation of the lower Murray River—the Victorian Mallee region. Victoria: Land Conservation Council unpublished report.

BARKHAM, J. P., 1992. Population dynamics of the wild daffodil (*Narcissus pseudonarcissus*). IV. Clumps and gaps. *Journal of Ecology* 80: 797–808.

BEATLEY, J. C., 1974. Phenological events and their environment triggers in Mojave Desert ecosystems. *Ecology* 55: 856–863.

BELL, D. T. & STEPHENS, L. J., 1984. Seasonality and phenology of Kwongan species. In *Kwongan, Plant Life of the Sandplain*, J. S. Pate & J. S. Beard, eds, University of Western Australia Press, Perth, 205–226.

BIERZYCHUDEK, P., 1982. Life histories and demography of shade-tolerant temperate forest herbs: a review. *New Phytologist* 90: 757–776.

BOEKEN, B. & GUTTERMAN, Y., 1989. *Tulipa systola*. In *CRC Handbook of Flowering* vol. VI, A. H. Halevy, ed., CRC Press, Boca Raton, 648–653.

BURTT, B. L., 1970. The evolution and taxonomic significance of a subterranean ovary in certain monocotyledons. *Israel Journal of Botany* 19: 77–90.

CALDWELL, M. L. H., 1969. *Erythronium*: comparative phenology of alpine and deciduous forest species in relation to environment. *American Midland Naturalist* 82: 543–558.

CHEAL, D. C. & PARKES, D. M., 1989. Mallee vegetation in Victoria. In *Mediterranean Landscapes in Australia*, J. C. Noble & R. A. Bradstock, eds, CSIRO, Melbourne, 125–140.

CHIN, H. F., 1988. *Recalcitrant Seeds. A Status Report*. International Board for Plant Genetic Resources, Rome.

CUNNINGHAM, G. M., MULHAM, W. E., MILTHORPE, P. L. & LEIGH, J. H., 1981. *Plants of Western New South Wales*. NSW Govt Printing Office, Sydney.

DAFNI, A., COHEN, D. & NOY-MEIR, I., 1981. Life-cycle variation in geophytes. *Annals Missouri Botanical Garden* 68: 652–660.

DAFNI, A., SHMIDA, A. & AVISHAI, M., 1981. Leafless autumnal-flowering geophytes in the Mediterranean region—phytogeographical, ecological and evolutionary aspects. *Plant Systematics & Evolution* 137: 181–193.

DAHLGREN, R. M.T ., CLIFFORD, H. T. & YEO, P. F., 1985. *The Families of the Monocotyledons*. Springer-Verlag, Berlin.

DANIN, A., 1983. *Desert Vegetation of Israel and Sinai*. Cana Publishing House, Jerusalem.

ELLIOT, W. R. & JONES, D. L., 1982. *Encyclopaedia of Australian Plants*, vol. 2. Lothian, Melbourne.

EVENARI, M., SHANAN, L. & TADMOR, N., 1971. *The Negev*. Harvard University Press.

FAHN, A. & CUTLER, D. F., 1992. *Xerophytes*. Gebrüder Borntraeger, Berlin.

GILBERT, O. L., 1989. *The Ecology of Urban Habitats*. Chapman & Hall, London.

GULLAN, P. K., CHEAL, D. C. & WALSH, N. G., 1990. *Rare or Threatened Plants in Victoria*. Department of Conservation & Environment, Melbourne.

GUNN, C. R. & DENNIS, J. V., 1976. *World Guide to Tropical Drift Seeds and Fruits*. Demeter Press, New York.

HANNIBAL, L. S., 1966. The *Crinum* genus. *Australian Plants* 3: 262–265.

HEWSON, H. J., 1987. *Crinum*. In *Flora of Australia*, A. S. George, ed., Australian Government Publishing Service, Canberra, 369–375.

HITCHMOUGH, J., 1989. *Garden Bulbs for Australia and New Zealand*. Viking O'Neil, Melbourne.

HOWELL, G., 1984. The reproductive biology of the Darling Lily, *Crinum flaccidum* Herb. B.Sc. Honours thesis, University of New England.

HOWELL, G. & PRAKASH, N., 1990. Embryology and reproductive ecology of the Darling Lily, *Crinum flaccidum* Herbert. *Australian Journal of Botany* 38: 433–444.

ISAAC, W. E. & McGILLIVRAY, G., 1965. A note on the water-storing seeds of two species of *Crinum* and of some other South African Amaryllidaceae. *Annals of Botany* 29: 739–740.

JESSOP, J., 1981. *Flora of Central Australia*. Reed, Sydney.

JOHNSON, S. D., 1993. Climatic and phylogenetic determinants of flowering seasonality in the Cape flora. *Journal of Ecology* 81: 567–572.

KOSHIMIZU, T., 1930. Carpobiological studies of *Crinum asiaticum* L. var. *japonicum* Bak. *Memoirs of the College of Science, Kyoto Imperial University*, Series B. 5: 183–227.

KOSHIMIZU, T., 1938. On the 'Crinum Line' in the flora of Japan. *Botanical Magazine* 52: 135–139.

LE MAITRE, D. C. & MIDGLEY, J. J., 1992. Plant reproductive ecology. In *The Ecology of Fynbos*, R. M. Cowling, ed., Oxford University Press, Cape Town, 135–174.

LOTHIAN, T. R. N., 1957. *Crinum flaccidum* (Murray or Darling Lily). *Journal of the Royal Horticultural Society* 82: 344–347.

LOTHIAN, T. R. N., 1969. South Australian plants with fleshy or bulbous rootstock (excluding orchids). *Australian Plants* 5: 77.

MANASSE, R. S., 1990. Seed size and habitat effects on the water-dispersed perennial, *Crinum erubescens*

(Amaryllidaceae). *American Journal of Botany* 77: 1336–1341.

MOORE, C. W. E., 1984. Annotated checklist of the vascular plants in part of northwestern New South Wales. CSIRO Australia Division of Water and Land Resources Technical Memorandum 84/30.

NAULT, A. & GAGNON, D., 1993. Ramet demography of *Allium tricoccum*, a spring ephemeral, perennial forest herb. *Journal of Ecology.* 81: 101–119.

NEWSTROM, L. E., 1989. Reproductive biology and evolution of the cultivated chayote *Sechium edule*: Cucurbitaceae. In *The Evolutionary Ecology of Plants*, J. H. Bock & Y. B. Linhart, eds, Westview Press, Boulder, 491–509.

OLIVER, I. B., 1990. *Crinum bulbispermum*: an interesting geophyte with horticulture potential. *Herbertia* 46: 52–53.

ORSHAN, G., 1989. Introduction. In *Plant Phenomorphological Studies in Mediterranean Type Ecosystems,* G. Orshan, ed., Kluwer, Dordrecht, 1–5.

PARSONS, W. T. & CUTHBERTSON, E. G., 1992. *Noxious Weeds of Australia*. Inkata Press, Melbourne.

PATE, J. S. & DIXON, K. W., 1982. *Tuberous, Cormous and Bulbous Plants*. University of Western Australia Press, Perth.

PIERCE, S. M. & COWLING, R. M., 1984. Phenology of fynbos, renosterveld and subtropical thicket in the south eastern Cape. *South African Journal of Botany* 3: 1–16.

PURDIE, R., 1984. Land systems of the Simpson Desert region. CSIRO Australia Division of Water and Land Resources. Natural Resources Series No. 2.

REES, A. R., 1972. *The Growth of Bulbs*. Academic Press, London.

RENNER, S. S., 1992. Seed dispersal. *Progress in Botany* 53: 435–453.

ROSS, J. H., 1993. *A Census of the Vascular Plants of Victoria*, 4th edn. National Herbarium of Victoria, Melbourne.

SCHNEIDER, R. L. & SHARITZ, R. R., 1988. Hydrochory and regeneration in a bald cypress—water tupelo swamp forest. *Ecology* 69: 1055–1063.

SHREVE, F. & WIGGINS, I. L., 1964. *Vegetation and Flora of the Sonoran Desert*. Stanford University Press, Stanford.

SNIJMAN, D., 1984. A revision of the genus *Haemanthus* L. (Amaryllidaceae). *Journal of South African Botany* Supplementary Volume No. 12.

SOLBRIG, O. T. & SIMPSON, B. B., 1977. Plants. In *Convergent Evolution in Warm Deserts,* G. H. Orians & O. T. Solbrig, eds, Dowden, Hutchinson & Ross, Stroudsburg, 53–56.

TELFORD, I. R. H., 1987. *Proiphys* and *Calostemma*. In *Flora of Australia*, A. S. George, ed., Australian Government Publishing Service, Canberra, 376–379, 382–383.

TOMLINSON, P. B., 1980. Monocotyledonous habit in relation to morphology and anatomy. In *Petaloid Monocotyledons*, C. D. Brickell, D. F. Cutler & M. Gregory, eds, Academic Press, London, 7–18.

VERDOORN, I. C., 1973. The genus *Crinum* in southern Africa. *Bothalia* 11: 27–52.

VICTORIA:: RURAL WATER COMMISSION, 1986a. Murray River flood plain management study. Detailed report. Rural Water Commission of Victoria, Melbourne.

VICTORIA: RURAL WATER COMMISSION, 1986b. Murray River flood plain atlas. Rural Water Commission of Victoria, Melbourne.

WILLIS, J. H., 1970. *A Handbook to Plants in Victoria*. 2nd edn. Melbourne University Press.

ZIMMER, W. J., 1946. The flora of the far north-west of Victoria. Forests Commission of Victoria Bulletin No. 2.

NEW RECORDS AND REDESCRIPTIONS OF THECATE HYDROIDS FROM SOUTHERN AUSTRALIA

JEANETTE E. WATSON

Honorary Associate, Museum of Victoria, 328 Swanston Street, Melbourne 3000

WATSON, JEANETTE E., 1994:12:31. New records and redescriptions of thecate hydroids from Australia. *Proceedings of the Royal Society of Victoria* 106: 147–162. ISSN 0035-9211.

Five species of hydroids formerly thought to be rare are redescribed and their ecology discussed. These are a hydroid doubtfully assigned to *Clytia hemisphaerica* Linnaeus, 1767, *Silicularia undulata* (Mulder & Trebilcock, 1914), *Thyroscyphus macrocytharus* (Lamouroux, 1824), *Clytia paulensis* (Vanhöffen, 1910), and the hydroid and medusa stages of *Phialella quadrata* (Forbes, 1848). Two other species, *Lafoeina amirantensis* (Millard & Bouillon, 1973) and *Aglaophenia postdentata* Billard, 1913 are new records for Australia.

COLLECTIONS (mostly by the author) along the southern Australian coastline have yielded five species of hydroids formerly thought to be rare in the region, and two new records for Australia.

Lafoeina amirantensis (Millard & Bouillon, 1973), and *Aglaophenia postdentata* Billard, 1913 are new records for Australia. *Lafoeina amirantensis* is recorded from Bass Strait in the south-east, and *A. postdentata* from the south-west of the continent. The hydroid of *Phialella quadrata* (Forbes, 1848), previously recorded as *Lovenella briggsi* Mulder & Trebilcock, 1915, is resdescribed together with two stages in the development of the medusa. *Clytia ?hemisphaerica* Linnaeus, 1767, and *Silicularia undulata* (Mulder & Trebilcock, 1914) were previously recorded from few Australian localities; these species are now known to be widespread across the southern continent. Although it was one of the earliest described hydroids from Australia, *Thyroscyphus macrocytharus* (Lamouroux, 1824) has been misidentified in the past: the species is here redescribed.

Material lodged in the Museum of Victoria is denoted by the prefix NMV.

Family Campanulinidae Hincks, 1868

Genus Lafoeina M. Sars, 1874

Calder (1991) discussed the systematic status of the closely related genera *Lafoeina* and *Egmundella* and because of their obscure family affiliations and the lack of information on their reproductive structures, excluded them from the Campanulinidae. He distinguished *Lafoeina* from *Egmundella* chiefly on the basis of its cylindrical and sessile or nearly sessile hydrotheca, the lack of a basal perisarcal shelf, and its oval nematophores. In *Egmundella*, hydrotheceae are conical and pedicellate, a perisarcal shelf is present and nematophores are tubular to

elavate. He referred material from Bermuda, corresponding to *Egmundella amirantensis* Millard & Bouillon, 1973 from the Indian Ocean, to *Lafoeina*.

Specimens from Bass Strait possess elavate nematotheceae which agree perfectly with Millard & Bouillon's description of *Egmundella amirantensis* but agree less well with Calder's figure (fig. 3, p. 10) of his Bermuda specimens. The hydranths of the Bass Strait specimens have a distinct base which rests upon the narrow floor of the hydrotheca but the perisarcal shelf is absent. Following Calder, the Bass Strait material is here referred to *Lafoeina*. However, until the relationships of *Lafaoeina* and *Egmundella* are better known, *Lafoeina* is provisionally retained in the Campanulinidae.

Lafoeina amirantensis (Millard & Bouillon, 1973)

Fig. 1A

Lafoeina amirantensis (Millard & Bouillon).—Calder, 1991: 10, fig. 3.

Egmundella amirantensis Millard & Bouillon, 1973: 40, fig. 5A–D.—Millard, 1975: 133, fig. 43G.—Garcia-Corrales, Arcas & De Diego, 1979: 27, fig. 14.—Roca, 1986: 9.—Gibbons & Ryland, 1989: 389, fig. 7.—Ramil & Vervoort, 1992: 22, fig. 2a–d.

Material and record. NMV F51790. Microslide. Ninety Mile Beach, Bass Strait, 38°13′S,147°13′E, 1 km offshore from Delray Beach, on the stems of *Tubularia exxonia* Watson, 1978, 10 m, N. W. Watson, 20/4/91.

Description. Hydrorhiza reptant, hydrotheceae variable in length, arising directly from the hydrorhiza on very short but distinct pedicel, a faint constriction of the perisarc separating hydrotheca from pedicel; hydrotheca narrowest at base, body cylindrical or widening slightly to margin, often narrowing just below origin of operculum. Oper-

culum consisting of approximately 10 long, sharply pointed segments, not clearly demarcated from margin. Hydranth with 10–14 tentacles, capable of considerable extension and deep withdrawal into the hydrotheca; base of hydranth seated on a slight

thickening of the perisarc immediately above the pedicel.

Nematothecae borne on the hydrorhiza, one between every three or four hydrothecae, clavate, maximum width about two-thirds the distance up
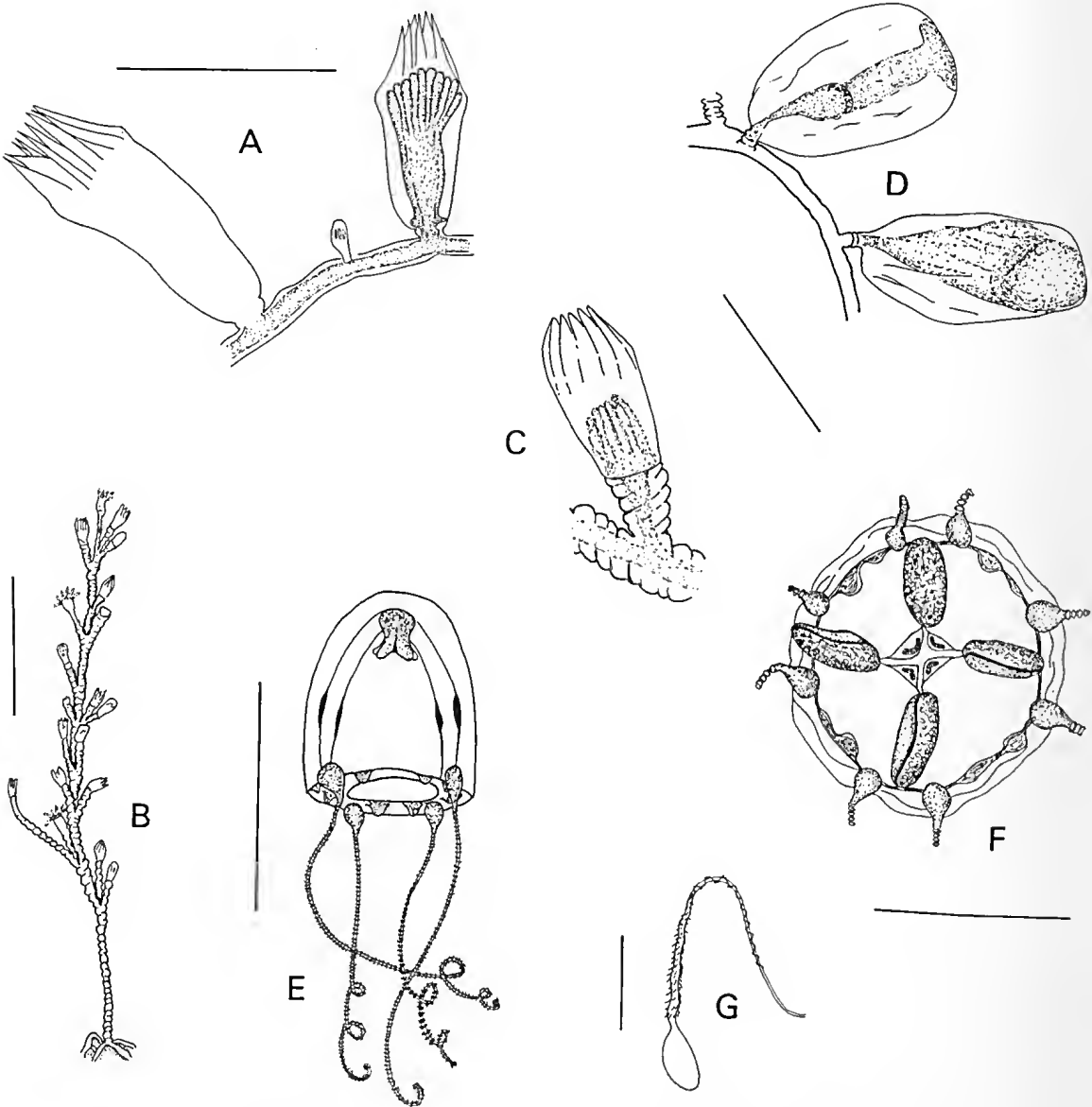
Fig. 1. A–F. A, *Lafoeina amirantensis*, part of colony from Bass Strait with hydrothecae and nematotheca. B–G, *Phialella quadrata*, mature stem from Western Port, Victoria. C, hydrotheca showing opercular segments. D, immature gonothecae. E, newly released medusa from colony from Western Port, living specimen. F, eight-tentacle stage medusa from Port Kembla, New South Wales, preserved material. G, discharged microbasic mastigophore from newly released medusa. Bar scales: A, C, D, 0.2 mm; B, E, 1 mm; F, 3 mm; G, 10 μm.

from base, body narrowing to a small circular orifice; several elongate nematocysts clustered inside.

Perisarc of colony very delicate and almost transparent, thinning distally on hydrotheca.

Measurements (mm). Width of hydrorhiza 0.05, length of hydrotheca from base to origin of operculum 0.14–0.27, width at margin 0.10–0.15, length of nematotheca 0.05–0.07, maximum width 0.02.

Remarks. The colonies were abundant on stems of *Tubularia exxonia* growing on a buoy-line. The rope had been immersed for a period of eight weeks, during which time it was heavily colonised by *T. exxonia*. *Lafoeina amirantensis* is an opportunistic shallow water epizooite of other hydroids (Millard & Bouillon 1973; Garcia-Corrales et al. 1979; Calder 1991; Ramil & Vervoort 1992) and is an occasional epiphyte of weed (Millard & Bouillon 1973). The record of Gibbons & Ryland (1989) from Fiji is also from a tubularian hydroid.

This is the first record of *Lafoeina* from Australia.

Family Phialellidae Russell, 1953

Genus Phialella Browne, 1902

The genus *Phialella* is known from five species (Boero 1987). These are: *Phialella quadrata* (Forbes, 1848), *Phialella hyalina* (von Lendenfeld, 1885), *Phialella falklandica* Browne, 1902, *Phialella fragilis* Uchida, 1938, and *Phialella zappai* Boero, 1987. *Phialella quadrata* is the most widely distributed of these species, being recorded from the Indo-Pacific, Japan, New Zealand, Chile and north-western Europe (Kramp 1968).

Phialella quadrata (Forbes, 1848)

Fig. 1B–G

Mulder & Trebilcock (1915) described the hydroid *Lovenella briggsi* from south-eastern Australia; it was next recorded as *Phialella briggsi* (Mulder & Trebilcock, 1915) from *Amphibolis* seagrasses by Watson (1992). Further collecting shows it to be a very common species in many southern Australian habitats.

I have compared microslide specimens of Mulder & Trebilcock's *L. briggsi* in the Museum of Victoria collection (NMV F57997, four microslides labelled 'Corio Bay'; F57998, three microslides, labelled Torquay) with fresh material and have found no features that distinguish it from *Phiallela quadrata*. I therefore refer *Lovenella briggsi* to *Phialella quadrata* (Forbes, 1848).

From records of the medusa of *P. quadrata* from New Zealand (= *Eucope annulata* von Lendenfeld, 1885, see Ralph 1957), Southcott (1982) presumed its range extended to southern Australia. Von Lendenfeld (1885b) also described a second medusa as *Eucope hyalina* von Lendenfeld, 1885, from Port Jackson, New South Wales. Kramp (1953) regarded *E. hyalina* as a distinct species but later doubted its validity (Kramp 1968, p. 84). I have examined the type material of *E. hyalina* held in the Australian Museum: it consists of fluid preserved material and one microslide preparation, mounted in Canada Balsam and labelled 'Type Y182'. The specimens in fluid have decomposed beyond recognition; the microslide consists of three reasonably well preserved medusae, two of which are arranged in lateral view and the other in transverse aspect. The medusae have eight tentacles and eight adradial vesicles. Only one statolith is visible near each adradial bulb, not three, as stated by von Lendenfeld. Medusae collected by the author from New South Wales near von Lendenfeld's type locality are clearly referrable to *P. quadrata* as described and figured by Kramp (1968), Russell (1953) and Boero (1987).

Kramp (1968) considered the medusa of *P. quadrata* to be conspecific with *P. fragilis* (Uchida, 1938) from Japan. Boero (1987) however, regarded them as distinct although very closely related species, the two main points of difference being the triangular tentacle bulbs of *P. fragilis* (those of *P. quadrata* being globular), the absence of nematocysts from the exumbrella, the quadrate manubrium and the absence of interradial tentacle bulbs on newly released *P. fragilis*. Manubria of very young medusae of *P. quadrata* examined in the present study were seen to rapidly change from quadrate to cruciform shape, depending upon the state of extension of the tentacles. At the same time, the tentacle bulbs changed shape from globular to triangular. Other than the absence of rudimentary interradial tentacle bulbs from *P. fragilis*, the hydroid and medusa phases of the two species are identical. However, until the taxonomic significance of the rudimentary interradial tentacle bulb is better known, *P. fragilis* and *P. quadrata* should be regarded as separate species.

The first three growth stages of the medusa of *P. quadrata* have been recorded in the present study. Liberation of large numbers of the earliest (four-tentacle) stage medusae from late summer colonies of *P. quadrata* from Western Port, Victoria, was observed in the laboratory; the eight-tentacle stage was found in abundance in summer plankton hauls in the harbour of Port Kembla, New South Wales and several medusae at the 16-

tentacle stage were collected in a late autumn (May) plankton haul from eastern Bass Strait.

The genus *Phialella* as now envisaged comprises *P. quadrata*, *P. fragilis*, *P. falklandica* and *P. zappai*.

The hydroid of *P. quadrata* and the two early medusa stages from Australia are described.

Thaumantiantias quadrata Forbes, 1848: 43, pl. 9, fig. 2.
Eucope annulata von Lendenfeld, 1885a: 602, pl. 28, figs 52–57.
Eucope hyalina von Lendenfeld, 1885b: 920, pl. 42, figs 16–18.
Lovenella briggsi Mulder & Trebileock, 1915: 57, pl. 9, figs 3–3f.
Phialella quadrata (Forbes).—Ralph, 1957: 848, fig. 8g–i. —Kramp, 1968: 84, fig. 226.—Southeott, 1982: 135, fig. 4.26d.

Material and records.   NMV F51791. Fertile colony, with newly released medusae, preserved material, Western Port, Vietoria, on the green alga *Caulerpa cactoides* 3 m, J. E. Watson, 2/1/92. NMV F51792. Medusa from plankton haul, subsurfaee, Port Kembla Harbour, New South Wales, J. E. Watson, 25/9/91.

Description of hydroid.   Colonies both stolonal and erect. Hydrorhiza tubular, loosely adherent to the substrate. Stems small, unfascicled, corrugated throughout, rarely with smooth patches, perisarc thicker proximally, becoming thinner distally.

Proximal stem region unbranched, branching thereafter pseudo-sympodial, but often two to four hydrothecae given off from the same stem internode. Pedicel of hydrotheca corrugated, perisarc thinning distally and widening gradually to merge into base of the hydrotheca.

Hydrotheca almost cylindrical distally, widening slightly to margin, a transverse to oblique diaphragm near the base and above it a circle of desmocytes at the point of attachment of the hydranth. Young hydrothecae with a conical operculum of about cight very delicate wedge-shaped segments with blunt apex, the opercular flaps opening to form the margin. Hydranth with about 16 long moniliform tentacles armcd with the same nematocysts as in the medusa (see below).

Gonothecae borne singly on hydrorhiza or hydrocauli, pedicel short, with one or two annulations, variable in shape from almost cylindrical to elongate top-shaped, widening distally, summit truncated, perisare thin and smooth, containing one medusa and sometimes one medusa bud. The distal perisarc ruptures at release of the medusa leaving a loose sheath of tissue protruding.

Measurements (mm).   Height of stem 5, proximal width 0.06–0.07, hydrothecal pedicel 0.13–0.3, proximal width 0.06–0.08, width at diaphragm 0.06–0.07, width at margin 0.08–0.10, distance from diaphragm to end of apertural flaps 0.15–0.21, height of gonothecae ineluding pediecl 0.62–0.80, maximum width 0.35–0.50.

Description of medusa.   Medusa at liberation dome-shaped, jelly thick, deeper than wide, velum broad, with four perradial tentacles with oval to triangular bulbs, tentacles long, moniliform when extended, with clusters of nematocysts. Four thin radial canals each with a rudimentary gonad in the distal third; four undeveloped interradial tentacle bulbs and eight adradial statocysts each with two statoliths on the ring canal. Manubrium saccate, mouth quadrate with four short lips and a few nematocysts. Four dark markings in the interradial position at base of the stomach. No umbilical canal and no exumbrellar nematocysts. Tentacular nematocysts microbasic mastigophores, shaft thick, with long spines, thread thin, spinous.

Preserved specimens at the eight-tentacle stage with elongate stomach and manubrium with slightly fluted lips; four characteristic interradial brown-black spots at the junction of peduncle with exumbrella. At this stage the gonads are hollow canoe-shaped structures occupying the distal third of the radial canals; some eontain ripe ova.

Measurements.   Four-tentacle stage medusa—height 1.5 mm, width 0.8 mm, length of manubrium 0.3 mm, capsule of tentacular nematocysts 7–9 μm × 4–7 μm, shaft to 15 μm, length of thread 100 μm. Eight-tentacle stage medusa—height, 2.8–3 mm.

Colour.   Colonies white to colourless. Medusa at liberation transparent, stomach and perradial tentacle bulbs yellow to pale brown. Older medusa (preserved material) clear, gonads white to creamy pink.

Remarks.   The hydrothecal diaphragm of the hydroid is usually transverse, but in some hydrothecae it is oblique. The diaphragm forms the junction between the pedicel and hydrotheca and is a point of weakness at which hydrothecae often break away. Distal stolonisation as described for *P. fragilis* by Boero (1987) is very common and appears to be a result of environmental stress to the colony.

Newly released medusae were sluggish during the 24 h of observation in the laboratory, spending much time motionless on the bottom of the vessel, slow exploration by the tentacles being interrupted by occasional feeble swimming movements. No scattered nematocysts were seen on the exumbrella of the medusa as reported for European *P. quadrata* by Russell (1953).

Eight-tentacle stage medusae were among a summer plankton haul from an industrial harbour on the central coast of New South Wales. The hydroid was not found in the harbour. Sixteen-

tentacle stage medusae were captured in a plankton haul by the author in eastern Bass Strait in May, 1992.

The hydroid of *P. quadrata* is very common in summer in southern Australia (Watson 1992), growing on a wide variety of algae, seagrasses and invertebrate substrates in ocean and bays to depths of at least 25 m. The only previous record of the medusa is from Sydney, New South Wales as *Eucope hyalina* (von Lendenfeld, 1885).

Family Campanulariidae Hincks, 1868

Genus Clytia Lamouroux, 1812

Clytia ?hemisphaerica (Linnaeus, 1767)

Fig. 2A–E

Medusa hemisphaerica Linnaeus, 1767: 1098.
Laomedea gracilis M. Sars, 1851: 138.
Clytia gracilis (M. Sars).—Stechow, 1924: 69; 1925: 212.—Cornelius & Östman, 1986: 165.—Calder, 1991: 54.
Campanularia johnstoni Alder.—Bale, 1924: 232.—Ralph, 1957: 820, 823, figs 1h–u, 2, 3a–f.—Pennycuik, 1959: 170.
Campanularia serrulata Bale, 1888: 757, pl. 12, fig. 4.—Stechow, 1919: 46, fig. M.—Calder, 1991: 56.
Phialidium hemisphaericum (Linnaeus). Russell, 1953: 285–294, pl. 16, fig. 1, pl. 17, fig. 6, text-figs 172–179.—Kramp, 1965: 60; 1968: 76, 150–152, fig. 201.

For world synonymy see Cornelius 1982: 73.

Material and records. NMV F51793. Hydroid colony, preserved material, Ninety Mile Beach, Bass Strait, Victoria, 6 m, on buoy line 1 km offshore from Delray Beach, R. C. Langley, 20/5/1992. NMV F51801. Medusae, preserved material, lower Port Phillip Bay, on red alga, 10 m, J. E. Watson, 17/7/92.

Description of hydroid. Hydrorhiza tubular, 0.05–0.10 mm wide, loosely reptant on substrate.

Stems simple, slender and fragile, sometimes branched once, with up to 15 proximal and 8–10 distal annulations, remainder of stem smooth or with groups of two to three annulations. Hydrotheca conical, expanding evenly from base to margin, circular to subcircular in cross section, basal chamber below diaphragm contiguous with hydrotheca, perisarc delicate, thinning towards margin. Margin with 8–10 evenly spaced teeth, cusps variable in shape from sharply pointed to blunt, with wide incisions between. Hydranth with 12–16 tentacles.

Gonothecae borne on the hydrorhiza on a slightly twisted pedicel, barrel-shaped, walls smooth or sometimes slightly undulated, distally truncate, a constriction just below the margin, summit

concave. Gonophore with one to three developing medusa buds, medusa released by rupture of the perisarc.

Measurements of hydroid (mm). Height of stems to 5, diameter of stems 0.07–0.10, length of hydrotheca 0.35–0.75, diameter of basal chamber 0.13–0.17, diameter at margin 0.27–0.55, height of marginal teeth 0.06–0.07, width of incision between teeth 0.08–0.09, length of gonotheca 0.55–1.00, width 0.35–0.50.

Description of medusa. Release of medusae was observed in the laboratory. At liberation the medusa is almost hemispherical, jelly relatively thick and velum broad; scattered nematocysts on the exumbrella or in a band encircling the middle of the exumbrella. Stomach short, manubrium broad, with four poorly defined lips armed with nematocysts. Radial canals narrow, rudimentary gonads situated in the middle of each canal. Ring canal narrow with four perradial tentacles arising from oval marginal bulbs, one rudimentary tentacle bulb between the perradials and eight adradial statocysts each with one statolith. Tentacles hollow, long and extensile, richly armed with nematocysts. Nematocysts on exumbrella and tentacles microbasic mastigophores, capsule bean-shaped, spinous, thread moderately thick and very long.

Measurements of medusa. Exumbrella 0.66 mm high, width 0.85 mm, capsule of nematocyst 7 × 2 μm, shaft 6 μm, minimum length of thread 90 μm.

Colour. Colonies colourless to translucent white. Medusa colourless, tentacle bulbs and stomach pale yellow.

Remarks—Hydroid. The dentition of the hydrothecal margin of the present material is quite variable, most hydrothecae in a colony having blunt teeth, sometimes with truncated cusps; some cusps are however, sharply pointed, and more rarely, slightly skewed. Hydrocauli are seldom branched, but when so, branching is by means of a secondary pedicel arising from the proximal section of the primary stem.

Clytia hemisphaerica (as *Campanularia johnstoni* Alder, 1856) has been recorded from subtropical Queensland (Pennycuik 1959) and the closely related *Clytia gracilis* (M. Sars, 1851) was recorded from Western Australia by Stechow (1924, 1925). I have examined a microslide specimen (Canada Balsam mounted) of *Campanularia serrulata* prepared by W. M. Bale, in the collection of the Museum of Victoria (NMV F58758), labelled 'Port Jackson 1888' and probably part of Bale's type series (Stranks 1993). Cornelius (1982) and Calder (1991) considered *C. serrulata* to be a synonym of *Clytia hemisphaerica*. Bale's specimen,

attached to a fragment of seagrass, consists of numerous proximally and distally annulated stems. Most are simple but several are forked one or more times. The hydrothecae have bluntly pointed teeth separated by deep saddle-shaped incisions similar to the present specimens: no skewing of the teeth is evident.

Many authors [e.g. Cornelius (1982, 1992), Calder (1991)], have attempted to distinguish between *Clytia hemisphaerica* and *Clytia gracilis* on morphology of the hydrothecae. Calder (1991) considered that the usually skewed marginal teeth and spirally ribbed gonotheca of *C. hemisphaerica* were sufficient to distinguish it from the rounded cusps and smooth gonothecal walls of *C. gracilis*. Conversely, Cornelius (1982), figured a hydrotheca of *C. hemisphaerica* with distinctly skewed teeth but later, (1992), described *C. gracilis* as having a hydrotheca with cusps pointing to one side.

The small, delicate hydrothecae and smooth to
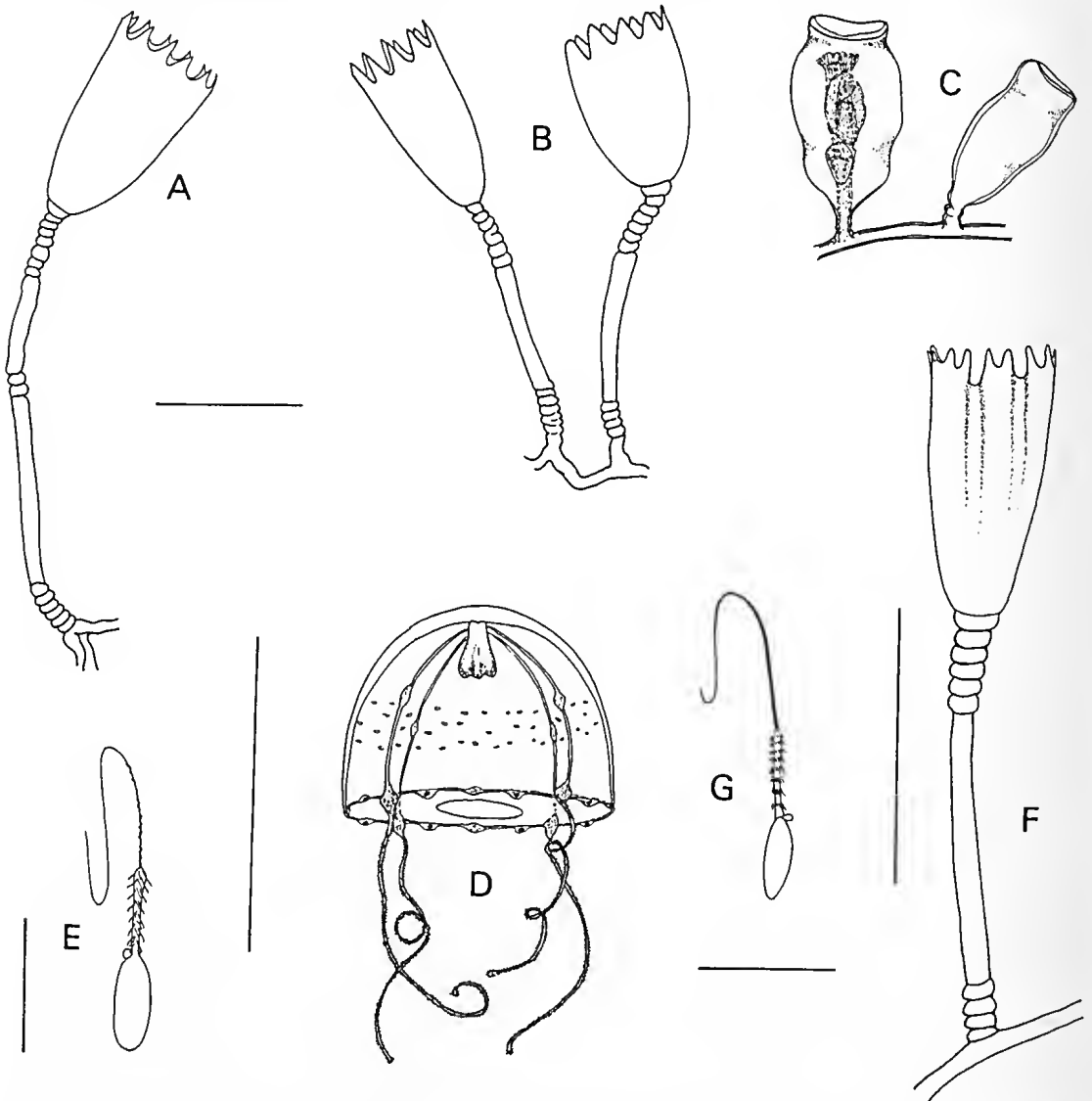
Fig. 2.   A–G, *Clytia hemisphaerica* from Port Phillip Bay. A, B, hydrothecae with rounded to pointed cusps. C, gonothecae. D, newly released medusa, living specimen. E, discharged microbasic mastigophore from medusa. F, G, *Clytia paulensis* from Port Phillip Bay, Victoria. F, hydrotheca. G, discharged microbasic mastigophore from hydranth. Bar scales: A–C, E, 0.5 mm; D, 1 mm; E, 10 μm.

faintly undulated gonothecae place the present specimens near *C. gracilis*; on the other hand, other characters such as the sometimes skewed teeth place it within the range of *C. hemisphaerica*.

In this state of taxonomic confusion it is impossible on colony morphology alone to assign the present material or Bale's *C. serrulata* to either *C. hemisphaerica* or *C. gracilis*. Cornelius & Östman (1986) and Östman (1987) were able to distinguish *C. hemisphaerica* from *C. gracilis* on the fine structure of the enidome. Thus until examination of the enidome of fresh material is carried out, the south-eastern Australian material is doubtfully assigned to *C. hemisphaerica*.

The hydroid is highly opportunistic, occurring on many invertebrate and red algal substrates and man-made structures. Colonies on natural substrates are usually small, comprising a few to tens of hydrocauli. In contrast, those on hard surfaces are often very prolific: for example, up to 50 hydrocauli per cm², and twice that number of gonothecae were counted on an experimental panel deployed for six weeks in Bass Strait (J. E. Watson, unpubl.). The hydroid is also abundant on drifting stems of the coastal seagrass *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog, and in this respect, resembles the pelagic colonies mentioned by Cornelius (1982).

Australian records are from the intertidal zone to 33 m deep. Distribution is from Western Australia to southern Queensland on algal substrates and the seagrasses *Halophila spinulosa* and *Amphibolis antarctica*, the alcyonarian *Telesto smithi* and on other hydroids (Stechow 1925; Pennycuik 1959; Watson 1992 and unpubl.).

Remarks—Medusa. The medusa of *C. hemisphaerica* has previously been recorded once, without description, from the Tasman Sea off the Australian continental shelf (Kramp 1965).

In a study of the life cycle of *Clytia edwardsi*, Kubota (1978) showed that the exumbrella nematocysts were arranged in a band in newly released medusae and were gradually shed with increasing maturity. He suspected, and Cornelius (1982) concurred, that *C. edwardsi* is conspecific with *C. hemisphaerica*. Kubota also reported three kinds of nematocysts in the medusa—two kinds of macrobasic mastigophores on the bell and lips and atrichous isorhizas in the tentacles. The resemblance between the three kinds of nematocysts (see Kubota 1978) may be the reason for their not being detected in the present material. Several medusae among the present specimens had five or six radial canals, and the bell was seen to frequently

contract into the characteristically quadrate shape described by Russell (1953).

Newly released medusae were sluggish, remaining contracted for long periods on the bottom of the vessel. At the same time however, the manubria were very active, exploring the inside of the bell.

Clytia paulensis (Vanhöffen, 1910)

Fig. 2F, G

Campanularia paulensis Vanhöffen, 1910: 298, fig. 19.
Clytia paulensis (Vanhöffen).—Stechow, 1919: 45, 155; 1923: 110, fig. N; 1925: 211.—Millard, 1975: 221, fig. 73a–d.—Cornelius, 1982: 88–91, fig. 14.

Material and record. NMV F51794 microslide Port Phillip Bay, on *Obelia australis* von Lendenfeld, 1885, 10 m, J. E. Watson 29/2/92.

Description. Hydrorhiza tubular, running up the stems and along the branches of the host. Pedicels given off at regular intervals, slender, tubular, perisarc smooth and glassy with 7–12 proximal and 4–9 distal deep annulations. Hydrotheca deep, conical, walls straight, expanding to margin. Margin with six pairs of bidentate teeth, each tooth with a slightly blunt apex, teeth sometimes inclined inwards, a shallow saddle separating each pair of cusps and a deep U-shaped incision between the pairs, often an indistinct ridge passing from the sides of the incision down into the hydrotheca. Hydranth with 12–16 tentacles held out stiffly in an amphicoronate arrangement from the hydrotheca. Tentacular nematocysts microbasic mastigophores, capsule elongate, shaft spinous, thread long.

Material sterile.

Measurements. Pedicels 0.65–0.82 mm long, diameter, 0.04–0.05 mm, length of hydrotheca, diaphragm to margin, 0.47–0.5 mm, width at margin 0.18–0.21 mm, depth of tooth from cusp to base, 0.04 mm. Capsule of tentacular nematocysts 5×1.5–2 μm.

Remarks. The only previous record of *Clytia paulensis* from Australia is that of Stechow (1924, 1925) who briefly described but did not figure a specimen from Shark Bay, Western Australia. The present specimens are larger than measurements given by Stechow (hydrotheca, 0.3 mm, marginal width, 0.13 mm) but fall within the range given by Millard (1975) for specimens from southern Africa.

Some stems of the present material are branched by means of a secondary pedicel given off below the distal annulations of the primary stem, the pedicel growing closely parallel to the primary stem.

Clytia paulensis is an epizooite of other hydroids; it has been recorded from *Obelia dichotoma* by Cornelius (1982), a close congener of *Obelia australis*. It also occurs on sponges in Port Phillip Bay, Victoria.

This is the second record of the species from Australia and the first from eastern Australia.

Genus Silicularia Meyen, 1834

Silicularia undulata (Mulder & Trebilcock, 1914)

Fig. 3A–F

Eucopella undulata Mulder & Trebilcock, 1914: 10, pl. 2, figs 5–7.
Silicularia undulata (Mulder & Trebilcock). — Bale, 1914: 87, 89; 1919: 327. — Blackburn, 1938: 324.

Material and records. NMV F51796 microslide. Whitfords Reef, Marmion, Western Australia, on *Amphibolis antarctica*, 3 m, J. E. Watson, April, 1986. NMV F51795 microslide Queenscliff, Victoria, on *Amphibolis antarctica*, 3 m, J. E. Watson, 21/1/1987.

Description. Hydrorhiza reticulating, flat and ribbon-like, with a wide stolonal canal and a delicate flange of perisarc at each side. Hydrothecal pedicels short, to 2 mm in height, thickest at junction with the hydrorhiza, otherwise of same diameter throughout. Pedicel terminating in a distal shoulder bearing a flattened spherule slightly narrower in diameter than pedicel. Perisarc of pedicel thick, deeply annulated throughout but sometimes with a short, smooth proximal section.

Hydrotheca bilaterally symmetrical, bowl-shaped, wider than deep (mean depth/width ratio 1:1.2), with a conspicuously thickened asymmetrical base, hydrothecal margin smooth, sloping obliquely to one side. Hydranth large, robust, with about 24 tentacles, too large to retract into the hydrotheca.

Colonies dioecious, gonothecae of both sexes large, irregularly circular to elongate oval, perisarc thick and slightly undulated, borne on a very short pedicel arising from the hydrorhiza, mature gonotheca flattened to the substrate. Aperture distal, subcircular, slightly depressed into the body, surrounded by a thickened rim and sealed by an operculum.

Mature female gonophore a large sporosac containing 15–20 ova with a smaller, developing gonophore below.

Measurements of *S. undulata* from Western Australia and Victoria are compared with those of *S. rosea* (author's collection) (Table 1).

Colour. White.

| | Measurements (mm): | | | |
| | *S. undulata* | | *S. rosea* | |
	Range	Mean	Range	Mean
Hydrorhiza				
Width	0.25–0.35	0.30	0.32–0.37	0.35
Pedicel				
Length	0.55–1.13	0.77	0.75–3.38	2.07
Distal width	0.09–0.13	0.10	0.12–0.22	0.20
Diam. of spherule	0.07–0.10	0.09	0.10–0.13	0.11
Hydrotheca				
Maximum depth	0.23–0.36	0.31	0.30–0.68	0.49
Maximum width	0.30–0.45	0.39	0.50–0.70	0.62
Gonotheca				
Length	1.03–1.50	1.23	1.80–1.90	1.82
Maximum width	1.13–1.58	1.29	0.75–1.35	1.05
Length of pedicel	0.08–0.13	0.10	0.20–0.30	0.25

Table 1. Comparison of dimensions of *Silicularia undulata* with *Silicularia rosea*. (N = 10)

Remarks. *Silicularia undulata* has been recorded from Victoria (Mulder & Trebilcock 1914) and from Spencer Gulf, South Australia (Blackburn 1938). Although Blackburn (1942), and Ralph (1956), cite New South Wales as a locality, there is no record of *S. undulata* ever having been found on the Australian east coast.

In their original description, Mulder & Trebilcock (1914), noted the association of the species with the seagrass '*Cymodocea zosterifolea*' [= *Amphibolis antarctica* (Labill.) Sonder et Aschers] and although Blackburn (1938) did not record a substrate at the Sir Joseph Banks Islands, his specimens probably also came from the extensive seagrass meadows at this locality.

Mulder & Trebilcock (1914) and Bale (1914, 1919), distinguished *Eucopella undulata* from the closely related *Eucopella campanularia* von Lendenfeld, 1883, by its annulated stems and decumbent gonothecae. *Eucopella campanularia* was considered by Ralph (1956), to be a temperate-water '*subtropica*' form of *Silicularia bilabiata* (Coughtrey, 1875) which was later synonymised in *Silicularia rosea* Meyen, 1834, by Millard (1968, 1971, 1977).

Study of material collected from the seagrass meadows of southern Australia shows that, while closely related to *S. rosea*, *S. undulata* is sufficiently different to warrant it being considered a distinct species. *Silicularia undulata* is a smaller species than *S. rosea*, the difference in size being constant over its geographic range. Its annulated stems and recumbent gonothecae further distinguish it from *S. rosea*.

In contrast to the open stolonal connections characteristic of the Campanulariidae, in *S. undu-*

lata each new stolon emerges from its predecessor through an orifice in the hydrorhizal perisarc similar to the emergence of a new pedicel (Fig. 3C).

The colonies are sparingly fertile, usually bearing fewer than four gonothecae. The gonotheca commences growth as an irregular, fan-shaped or cornucopia-like bud from the hydrorhiza, later bending towards, and spreading on the seagrass leaf until at maturity it reclines upon a wide shelf of perisarc. Irregularities in shape of the mature gonotheca result from encountering obstructions during the prostrate stage of growth (Watson 1992).

Ralph (1956) and Harris (1990) showed that the gonophore of *S. rosea* is eumedusoid in structure. Examination of fresh material of *S. undulata* suggests that the gonophore of this species may be
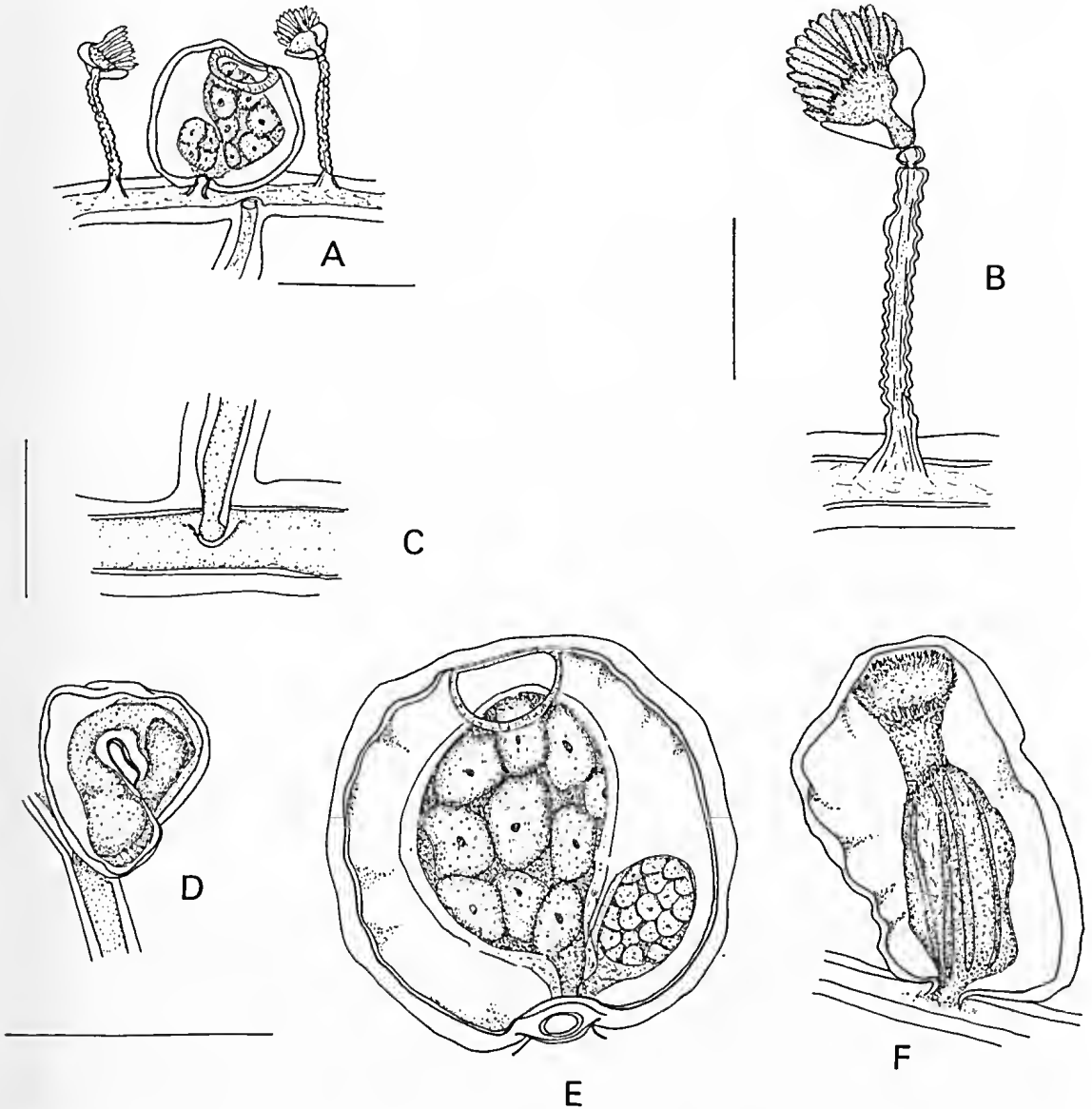
Fig. 3. A–F, *Silicularia undulata* from Marmion, Western Australia. A, part of female colony. B, hydrotheca fully retracted hydranth. C, hydrorhiza showing junction of stolonal canals. D, young gonotheca budding from hydrorhiza. E, mature female gonotheca with gonophore. F, mature male gonotheca with gonophore. Bar scales: A, D–F, 1 mm; B, C, 0.5 mm.

cryptomedusoid. It commences growth as a clearly recognisable hydranth which later degenerates, swelling to accommodate the sporosac while the aborted tentacles plug the aperture until release of the gametes.

An unusually large number of nematocysts of two kinds are always present in the hydrorhiza and hydrocaulus, a phenomenon also noted in some species of *Eudendrium* (Watson 1985). Both kinds of nematocysts are long and cigar-shaped, the larger being 15 μm long and 2–3 μm wide, and the smaller 6 × 1–2 μm. None were discharged.

Ecology and distribution. *Silicularia undulata* is a seagrass obligate endemic to Australia (Watson 1992). The weakly adherent hydrorhiza restricts the colonies to the most sheltered microhabitat in the axils of the seagrass leaves. Small colonies consisting of a few hydrocauli with short, robust stems, asymmetrical hydrothecae tilted to optimise water flow across the tentacles and gonothecae strongly recumbent to the substrate are adaptations necessary to survive the rigors of the seagrass habitat (Watson 1992).

Its congener, *S. rosea,* has southern circumpolar distribution (Ralph 1956). In southern Australia it is a common epiphyte of the brown algae *Scytothalia dorycarpa, Seirococcus axillaris* (R. Brown ex. Turner) Greville, *Ecklonia radiata* (C. Agardh) J. Aghardh and *Phyllospora comosa* (Labillardière). C. Agardh (see Shepherd & Watson 1970; Watson, unpubl.). *S. undulata* may be an example of speciation from the widespread parent *S. rosea* stock into the more specialised habitat of the seagrass meadow.

Family Thyroscyphidae Mammen, 1965

Genus Thyroscyphus Allman, 1877

Thyroscyphus macroeytharus (Lamouroux, 1824)

Fig. 4A, B

Lamouroux (1824) described *Clytia macrocythara* from material collected by the voyage of the *Uranie* and *Physicienne* to south-western Australia. Billard (1909) gave dimensions of the species held in the Lamouroux collection of l'Institut Botanique de Caen. Bale (1884) described *Campanularia marginata* from south-eastern Australia, distinguishing it from *Clytia macrocytharus* by its erect hydrocauli with three to four stem internodes, compared with the single stem internode of *Campanularia marginata*. The reproductive structures of neither species was then known.

Obelia marginata Allman, 1877, a similar but taller species with erect stems from the Atlantic, has been variously referred to *Campanularia* by Nutting (1915), to *Lytoscyphus* by Ritchie (1909) and Billard (1910), and to *Cnidoscyphus* by Splettstösser (1929). Recently, Calder (1983), assigned Allman's species to *Thyroscyphus* and renamed Bale's junior secondary homonym, *Thyroscyphus balei.* The finding of abundant fertile colonies with simple and compound stems in southwestern Australia (Borowitzka et al. 1989; Watson 1992) now permits reappraisal of the status of Bale's and Lamouroux's species. I have examined a series of Bale's Canada Balsam mounted microslides of *Campanularia marginata* from Bondi Bay, New South Wales, and from Queenscliff and Portland, Victoria, held in the Museum of Victoria. The Victorian specimens (NMV F58791 and F58792) are considered by Stranks (1993) to be probable syntypes. Other than complexity of the hydrocaulus there are no morphological differences that distinguish *C. macrocythara* from *C. marginata. Thyroscyphus balei* (= *C. marginata*) is thus considered a synonym of *Thyroscyphus macrocytharus.*

Clytia macrocythara Lamouroux, 1824: 647, pl. 93, figs 4, 5. — Lamarck, 1837: 199.
Campanularia marginata Bale, 1884: 54, pl. 1, fig. 2; 1888: 758. — Bartlett, 1907: 62. — Levinsen, 1913: 289.
Laomedea marginata (Bale). — von Lendenfeld, 1885: 404.
Campanularia macrocythara (Lamouroux). — Billard, 1909: 311.
Thyroscyphus marginatus (Bale). — Bale, 1914: 91; 1915: 245, 258. — Stechow, 1924: 69; 1925: 217. — Blackburn, 1942: 112. — Watson, 1973: 169. — Harris, 1990: 232–260.
Thyroscyphus balei Calder, 1983: 16. — Watson, 1992: 220.
Non Thyroscyphus marginatus (Allman, 1877). (See Calder 1983: 16, 1991: 79, for synonymy.)

Material and records. NMV F51800, microslide. Whitfords Reef, Marmion, Western Australia, 4 m, on stems of *Amphibolis antarctica,* J. E. Watson, 30/1/1986.

Description. Colonies creeping, hydrorhiza tubular, undulating. Stems arising as an extension of the hydrorhiza, either simple with a single terminal hydrotheca or erect, and bearing up to six hydrothecae. Cauline internodes long and straight, perisarc usually undulating, sometimes smooth, widening to a distal apophysis. Hydrothecae on compound hydrocauli usually all facing the same side of stem, each borne on a very short, narrow pedicel from the stem apophysis. Hydrothecae very large, campanulate, expanding evenly from base to margin, the hydranth supported on a distinct, flattened shelf above base. Margin circular to

somewhat quadrangular, with heavily thickened rim, a deeply indented submarginal ring below margin and four equidistant low, blunt marginal teeth. A low operculum of four equal triangular valves present in young hydrothecae. Hydranth very large and robust with about 20 short, stubby tentacles. Gonotheca borne on a short pedicel arising from the internode immediately below the hydrothecal apophysis, barrel-shaped, often asymmetrical with one side more convex than the other, walls broadly undulating, maximum diameter just below mid-region, distal end truncated, summit
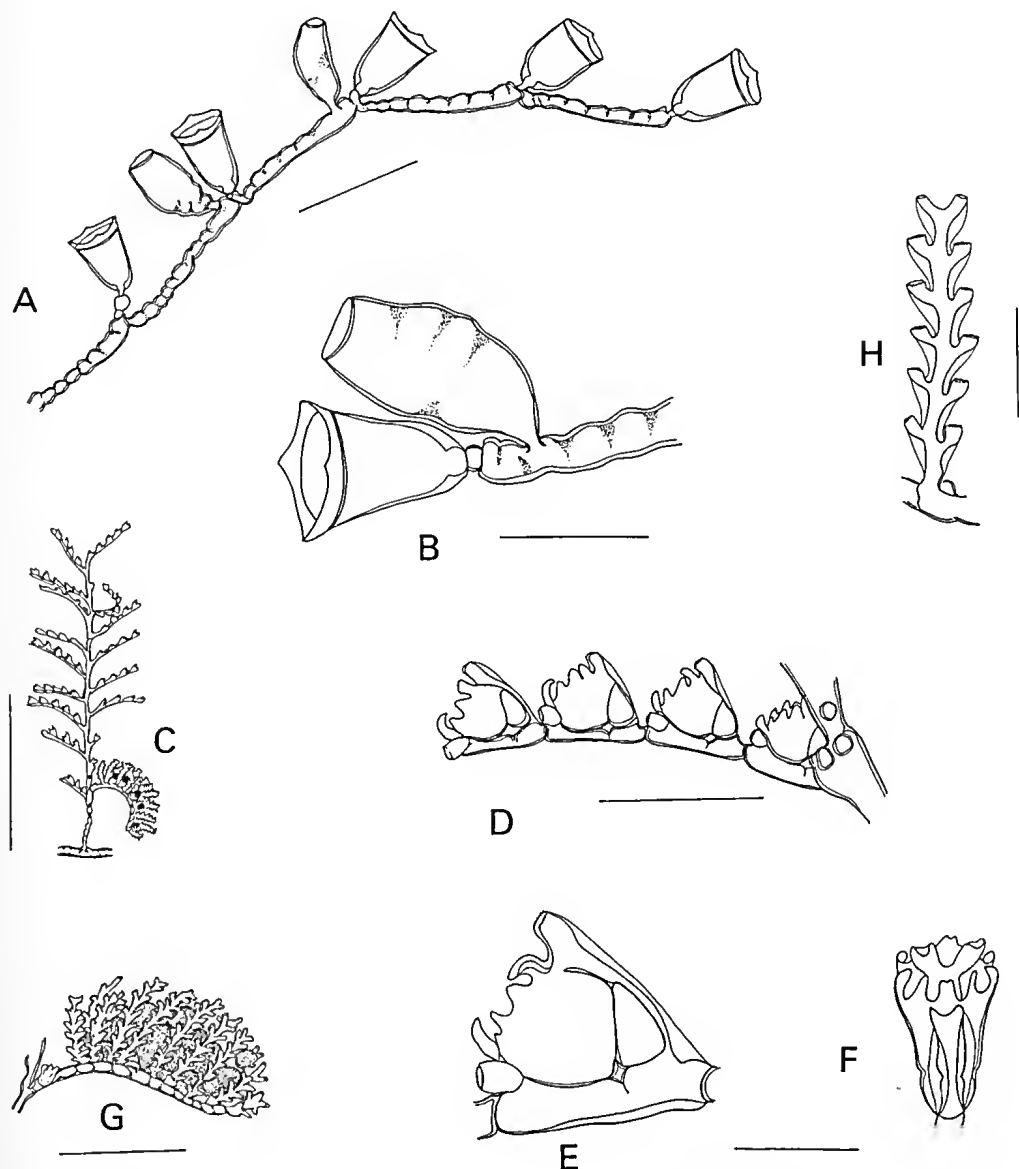
Fig. 4. A–H. A, B, *Thyroscyphus macrocyatharus* from Marmion, Western Australia. A, part of colony. B, hydrotheca and gonotheca from same colony, enlarged. C–F, *Aglaophenia postdentata* from Marmion, Western Australia. C, fertile stem. D, part of hydrocladium. E, hydrotheca, lateral view. F, hydrotheca, anterior view. G, corbula with mature gonophores. H, corbula rib. Bar scales: A, 2 mm; B, G, 1 mm; C, 4 mm; D, 0.5 mm; E, F, 0.2 mm.

often depressed, without aperture. Female gono-
phore a fixed sporosac containing two or three
large ova surmounted by a plug of tissue. Male
gonophore unknown.

Measurements (mm).   Width of hydrorhiza 0.28–0.65,
height of stems to 15, length of cauline internodes 1.90–
2.75, width at distal apophysis 0.18–0.39, depth of
hydrotheca from base to margin 1.05–1.35, diameter of
basal shelf 0.37–0.59, height above base of hydrotheca
0.09–0.18, diameter at margin 0.53–0.57, submarginal
ring 0.10–0.18 below margin, length of gonotheca 1.50–
1.63, maximum diameter 0.80–0.81, width at summit
0.50–0.58.

Colour.   Perisarc brown, hydranth often yellow;
colony frequently overgrown by pink crustose
coralline algae.

Remarks.   The hydrotheca of *T. macrocytharus*
is one of the largest Australian hydroids. The di-
mensions given by Billard (1909), for Lamouroux's
type material indicate a shorter, but wider hydro-
theca and shorter stem internodes.

In addition to the strongly developed floor
supporting the hydranth, there is a second internal
shelf in the hydrotheca about one third the distance
up from the base. This shelf probably provides a
supplementary anchorage for the very large and
heavy hydranth. A detailed account of the physi-
ology, adaptations and growth of *T. macrocytharus*
(as *T. marginatus*) is given by Harris (1990).

The perisarc of the colonies is unusually thick
throughout, imparting a woody brittleness to the
hydrocauli and many show evidence of repeated
breakage and regeneration. The species is very
abundant on the stems of *Amphibolis* seagrasses
in south-western Australia which habitat it shares
with *Stereotheca elongata* (Lamouroux, 1816) (see
Watson 1992).

The species is less common in cool temperate
southern Australia where colonies are usually small
and sterile (Watson 1973 and unpubl.). The deepest
record of *T. macrocytharus* is from 137 m, off the
coast of South Australia (Bale 1915). Stechow's
(1925) record is from 3–14 m on algae, from
Geraldton, Western Australia.

The finding of *T. macrocytharus* in the same
region of Western Australia as its presumed type
locality, confirms Lamarck's (1837) ecological note
of 'Habite sur le *Zostera antarctica* sur les côtes
de l'Australasie'.

Family **Aglaopheniidae** Broch, 1918

Genus **Aglaophenia** Lamouroux, 1812

Aglaophenia postdentata Billard, 1913

Fig. 4C–H

Aglaophenia postdentata Billard, 1913: 100, fig. 89. —
Jäderholm, 1920: 8, pl. 2, fig. 8. —Vervoort, 1941:
231. —Redier, 1966: 97, pl. 3, fig. 4. —Millard &
Bouillon, 1973: 90, fig. 11G, H. —Ryland & Gibbons,
1991: 557, fig. 24A–D.

Material and records.   NMV F51799. Microslide, female
colony, 6 km off Marmion, Perth, Western Australia,
on *Thalassodendron pachyrhizum* leaves, 24 m, J. E.
Watson, 30/1/1986.

Description.   Hydrorhizal stolons long, straight
and tubular, intersecting at regular intervals, sides
flattened and extended into delicate flanges loosely
adherent to the substrate, mature hydrorhiza with
regular flexion joints (see below) extending into
the stolon. Hydrocauli pinnate, unfascicled and
unbranched, proximal two or three internodes
athecate, with thick perisarc and strong, oblique
hinge joints, basal internode without nematothecae,
the following one or two internodes each with a
single nematotheca in the proximal third. Succeed-
ing cauline internodes slender, perisarc thick, nodes
usually an indistinct transverse constriction just
above the hydrocladial apophysis. Hydrocladia
alternate, given off from the apophyses on the front
of the stem, short, usually with six short thecate
internodes with distinct transverse joints. Hydro-
theca small, occupying the entire internode, axis
at an acute angle to the internode, posterior
angular, adcauline wall flat to slightly convex,
abcauline wall a smooth, convex curve, an intra-
thecal septum directed slightly backwards between
the adcauline and abcauline walls. Margin with
10 apertural teeth: four paired lateral teeth and two,
unpaired, one in the abcauline, and one in the
adcauline median position. Abcauline median tooth
almost rectangular in outline (anterior view),
obscured in lateral view. First paired lateral teeth
(abcauline view) leaf-shaped, margins outrolled,
each tooth arched inwards over the hydrothecal
aperture; second and third paired teeth broadly
lobed with deep embayments between, the fourth
pair shorter, lobe-shaped, situated behind the
lateral nematothecae (difficult to see in lateral
view), median adcauline tooth similar to median
abcauline, but much longer and arched inwards
over the aperture, edges rolled upwards. Median
nematotheca closely adnate to the hydrotheca,
distal end free from hydrotheca, abcauline wall
straight, adcauline wall slightly swollen, canalicu-
late, with a ragged, truncate margin, the open side
extending down to join the hydrotheca; a flange
of perisarc connecting the distal end with the
preceding hydrocladial node. Twin lateral nemato-
thecae the same shape as cauline nematothecae,
not extending past hydrotheca, one orifice circular,
facing forward, with a second orifice into the

hydrotheca. Cauline nematothecae of same shape as the laterals, one on the proximal part of the internode and two side by side on the hydrocladial apophysis.

Colonies dioecious, corbulae numerous, usually borne in the proximal stem region but sometimes distal. Gonohydrocladium replacing a hydrocladium, arched backwards, with one proximal hydrothecate internode followed by six or seven, but sometimes up to 15 ribs. Gonohydrocladial internodes oblique, distinct, each bearing a pair of corbula ribs with a single nematotheca at the base. Ribs free from base, arching over to meet at the top, with six or seven pairs of opposite to sub-opposite nematothecae similar to laterals, apertures ragged and facing upwards, the outside of each pair connected to the inner side of the preceding pair by a thin flange of perisarc. Gonothecae small, lenticular, the female containing about six small ova.

Measurements (mm). Width of hydrorhiza including flanges 0.32–0.35, flexion joints extending 0.05 mm into stolon. Height of hydrocauli 10, length of proximal cauline internodes 0.75–1.13, succeeding internodes 0.30–0.45, width at nodes 0.06–0.08, length of hydrocladial internodes 0.28–0.35, width at nodes 0.04–0.05, length of hydrotheca posterior to marginal teeth 0.24–0.28, internal width at septum 0.10–0.12, maximum internal width 0.14–0.19, width at margin 0.16–0.19, length of unpaired adcauline marginal teeth (lateral view) 0.033–0.048, length of median nematotheca 0.31–0.35, length free from hydrotheca 0.04–0.06, width of adcauline side 0.04, width of terminal orifice 0.05; length of corbulae to 3, length of gonohydrocladium 0.70–0.75, width across rib 0.20–0.25.

Colour. Colonies yellow in life; gonophores pink.

Remarks. Aglaophenia postdentata was first recorded from Australia by Watson (1992), from *Amphibolis* seagrasses and *Thalassodendron pachyrhizum* den Hartog, near Perth, Western Australia.

The dark markings which penetrate the hydrorhizae of many species are highly developed in *A. postdentata*. Several authors (Ritchie 1911; Philbert 1935; Picard 1952; Ralph 1961) have speculated on these markings and Watson (1973) considered them to be a response to life on a flexible substrate. Detailed examination of these 'flexion joints' shows them to be small, hollow, roughly key-hole shaped structures that penetrate the hydrorhiza from its outer edge to the stolonal canal: such joints are an excellent adaptation to relieve mechanical stress and thus prevent fracture of the hydrorhiza.

The most characteristic feature of *A. postdentata* and the one used by Billard (1913) to distinguish

it from *Aglaophenia pluma* (Linnaeus, 1758), is the very long median adcauline tooth of the hydrothecal margin. In the present material, this tooth is much longer than that figured by Billard (1913). The manner in which this, and the other apertural teeth arch over the hydrotheca, and the outrolled, leaf-shaped paired laterals, is diagnostic of the species. However, without careful examination from all angles these features are often very difficult to see.

New colonies commence growth from a small stolonal plate (Watson 1973) which spreads over the surface of the host, projecting a single stolon that matures into the hydrorhiza.

The hydrothecae of *A. postdentata* are morphologically uniform, there being no increase in the length of the median hydrothecal nematotheca distally along the hydrocladium as occurs in some aglaophenian hydroids. The wide, ragged terminal orifices of the median and gonohydrocladial nematothecae, which appear on casual inspection to be broken edges, are a constant and characteristic feature of *A. postdentata*.

Hydrocauli of *A. postdentata* from Australia are taller than those reported by Millard & Bouillon (1973) from the Seychelles. Since the corbulae of their material consisted of only two or three ribs compared with the six to 15 in the Australian specimens, it is likely that the Seychelles specimens were immature.

Aglaophenia postdentata is a tropical species previously recorded from north-western New Guinea and the Makassar Straits (Billard 1913), the Java Sea (Jäderholm 1920; Vervoort 1941) the Seychelles in the northern Indian Ocean (Millard & Bouillon 1973), and Fiji (Ryland & Gibbons 1991). The extension of the range of *A. postdenta* from the tropical Indo-Pacific to south-western Australia suggests larval transport southwards along the Western Australian coast by the Leeuwin current (Cresswell 1991).

REFERENCES

ALLMAN, G. J., 1877. Report on the Hydroida collected during the exploration of the Gulf Stream by L. F. de Pourtales, assistant, United States coast survey. *Memoirs of the Museum of Comparative Zoology, Harvard* 5: 1–66.

BALE, W. M., 1884. *Catalogue of the Australian hydroid zoophytes.* Australian Museum: Sydney, 117 p.

BALE, W. M., 1888. On some new and rare Hydroida in the Australian Museum collection. *Proceedings of the Linnean Society of New South Wales* 3(2): 745–799, pls 12–21.

BALE, W. M., 1914. Report on the Hydroida collected in the Great Australian Bight and other localities. *F.I.S. 'Endeavour' Report* 2: 1–62, pls 1–7.

BALE, W. M., 1915. Report on the Hydroida collected in the Great Australian Bight and other localities. *F.I.S. 'Endeavour' Report* 3: 241–336, pls 46, 47.

BALE, W. M., 1919. Further notes on Australian hydroids — IV. *Proceedings of the Royal Society of Victoria* 31(2): 327–361, pls 16, 17.

BALE, W. M., 1924. Report on some hydroids from the New Zealand coast with notes on New Zealand hydroids generally, supplementing Farquhar's list. *Transactions of the New Zealand Institute* 55: 225–268.

BARTLETT, G. C., 1907. Notes on hydroid zoophytes. *Geelong Naturalist* 3(4): 35–45.

BILLARD, A., 1909. Revision des espèces types d' hydroïdes de la collection Lamouroux conservée à l'Institut Botanique de Caen. *Annales des Sciences Naturelles (Zoology)* 9: 307–336.

BILLARD, A., 1910. Revision d'une partie de la collection des hydroïdes du British Museum. *Annales des Sciences Naturelles (Zoology)* 11(9): 1–67.

BILLARD, A., 1913. Les hydrode l'expédition du Siboga. 1. Plumulariidae. *Siboga Expedition* 7a: 1–115.

BLACKBURN, M., 1938. The Hydrozoa of the Sir Joseph Banks Islands. *Proceedings of the Royal Society of Victoria* 50(2): 312–328.

BLACKBURN, M., 1942. A systematic list of the hydroids of South Australia with a summary of their distribution in other seas. *Transactions of the Royal Society of South Australia* 66(1): 104–118.

BOERO, F., 1987. Life cycles of *Phialella zappai* n. sp., *Phialella fragilis* and *Phialella* sp. (Cnidaria, Leptomedusae, Phialellidae) from central California. *Journal of Natural History* 21: 465–480.

BOROWITZKA, M. A. & LETHBRIDGE, R. C., 1989. Seagrass epiphytes. In *Biology of seagrasses: a treatise on seagrasses with special reference to the Australian region*, A. W. D. Larkum, A. J. McComb & S. A. Shepherd, eds, Elsevier. p. 458–484.

BROCH, H., 1918. Hydroida. (Part II). *Danish Ingolf Expedition* 5(7): 1–206, figs 1–95, pl. 1.

BROWNE, E. T., 1902. A preliminary report on the hydromedusae from the Falkland Islands. *Annals and Magazine of Natural History* 9(7): 272–284.

CALDER, D. R., 1976. Biotic census of Cape Cod Bay: hydroids. *Biological Bulletin* 149: 287–315.

CALDER, D. R., 1983. Hydroida from estuaries of South Carolina, U.S.A: families Sertulariidae and Plumulariidae. *Proceedings of the Biological Society of Washington* 96(1): 7–28.

CALDER, D. R., 1991. Shallow-water hydroids of Bermuda: the Thecatae, exclusive of Plumularioidea. *Life Science Contributions 154, Royal Ontario Museum*, 140 p.

CORNELIUS, P. F. S., 1982. Hydroids and medusae of the family Campanulariidae recorded from the eastern North Atlantic, with a synopsis of genera. *Bulletin of the British Museum of Natural History, Zoology* 42(2): 37–148.

CORNELIUS, P. F. S. & ÖSTMAN, C., 1986. On the names of two species of the genus *Clytia* Lamouroux, 1812 (Coelenterata, Hydroida) common in Western Europe. *Bulletin of Zoological Nomenclature* 43: 163–169.

COUGHTREY, M., 1875. Notes on the New Zealand Hydroideae. *Transactions and Proceedings of the New Zealand Institute* 7: 281–293, pl. 20.

CRESSWELL, G. R., 1991. The Leeuwin current — observations and recent models. *Journal of the Royal Society of Western Australia* 74: 1–14.

FORBES, E., 1848. *A monograph of the British naked-eye medusae: with figures of all the species.* Ray Society, London.

GARCIA-CORRALES, P., ARCAS, V. B. & DE DIEGO, M., 1979. Contribucion al conocimiento de los hidrozoos de las costas espanolas. Parte II. Lafoeidae, Campanulinidae and Synthecidae. *Boletin del Instituto Espanol de Oceanography* 5(273): 5–39, figs 1–18.

GIBBONS, M. J. & RYLAND, J. S., 1989. Intertidal and shallow water hydroids from Fiji. 1. Athecata to Sertulariidae. *Memoirs of the Queensland Museum* 27(2): 377–432.

HARRIS, V. A., 1990. *Sessile animals of the seashore.* Chapman & Hall, London. p. 1–379.

JÄDERHOLM, E., 1920. On some exotic hydroids in the Swedish Zoological State Museum. *Arkiv för Zoologi* 13(3): 1–11.

KRAMP, P. L., 1953. Hydromedusae. — *Scientific Report, Great Barrier Reef Expedition 1928–29* 6(4): 259–322, pls 1, 2.

KRAMP, P. L., 1965. The hydromedusae of the Pacific and Indian Oceans. *Dana Report* 63: 1–161.

KRAMP, P. L., 1968. The hydromedusae of the Pacific and Indian Oceans (II & III). *Dana Report* 72: 1–200.

KUBOTA, S., 1978. Notes on *Clytia* and *Phialidium* (Hydrozoa: Campanulariidae) from Shimoda, Japan. *Proceedings of the Japanese Society of Systematic Zoology* 15: 1–7.

LAMARCK, J. P. B. A. DE, 1837. *Histoire naturelle des animaux sans vertèbres.* 3rd edn. Bruxelles.

LAMOUROUX, J. V. F., 1812. Extrait d'un mèmoires des polypiers coralligènes non entièrement pierreux. *Nouveau Bulletin des Sciences par la Société Philomatique de Paris* 3: 181–188.

LAMOUROUX, J. V. F., 1816. *Histoire des Polypiers coralligènes flexibles, vulgairement nommés Zoophytes.* Caen: F. Poisson. 1–559.

LAMOUROUX, J. V. F., 1824. Polypiers flexibles. In *Voyage autour du monde (exécuté sur les corvettes de S. M. l'Uranie et la Physicienne, pendant les anneés 1817, 1819 et 1820, par M. Louis de Freycinet)*. J. R. C. Quoy & J. P. Gaimard. Zoologie: 603–693. Paris: Pillet.

LENDENFELD, R. VON, 1883. Über Coelenteraten de Südsee 4. Mittheilung *Eucopella campanularia* nov. gen. *Zeitschrift für wissenschaftliche Zoologie* 38(4): 497–582, pls 27–32.

LENDENFELD, R. VON, 1885a. The Australian Hydromedusae. 5. *Proceedings of the Linnean Society of New South Wales* 9(3): 581–634, pl. 28, figs 53–57.

LENDENFELD, R. VON, 1885b. Addenda to the Australian Hydromedusae. *Proceedings of the Linnean Society of New South Wales* 9(4): 908–924, pl. 42, figs 16–18.

LEVINSEN, G. M. R., 1913. Systematic studies on the Sertulariidae. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjobenhavn.* Bd. 64: 259–321, pls 4, 5.

LINNAEUS, C., 1758. *Systema naturae.* Ed. 10. Holmiae.

LINNAEUS, C., 1767. *Systema naturae.* Ed. 12. Holmiae.

MAMMEN, T. A., 1965. On a collection of hydroids from South India. II. Suborder Thecata (excluding family Plumulariidae). *Journal of the Marine Biological Association of India* 7: 1–57.

MEYEN, F. J. F., 1834. das Leuchten des Meeres und Beschreibung einiger Polypen und anderer neiderer Thiere. *Nova Acta Acadamie Caes Leopold-Carol* 16 (Suppl.).

MILLARD, N. A. H., 1968. South African Hydroids from Dr Th. Mortensens's Java–South Africa Expedition, 1929–1930. *Viddenskabelige Meddelelser Fra Dansk Naturhistorisk Forening* 131: 251–288.

MILLARD, N. A. H., 1971. Hydrozoa. In *Marion and Prince Edward Islands.* E. M. Zinderen Bakker, J. M. Winterbottom & R. A. Dyer, eds. A. A. Balkena, Cape Town. p 396–408.

MILLARD, N. A. H., 1975. Monograph on the Hydroida of southern Africa. *Annals of the South African Museum* 68: 1–513.

MILLARD, N. A. H., 1977. Hydroids from the Kerguelen and Crozet shelves, collected by the cruise MD.03 of the 'Marion-Dufresne'. *Annals of the South African Museum* 73(1): 1–47.

MILLARD, N. A. H. & BOUILLON, J., 1973. Hydroids from the Seychelles (Coelenterata). *Annales de Musee Royal de L'Afrique Centrale, (Belg) Sciences* (Zool.) 206: 1–106.

MULDER, J. F. & TREBILCOCK, R. E., 1914. Victorian Hydroida with description of new species. *Geelong Naturalist* 6(2): 38–47.

MULDER, J. F. & TREBILCOCK, R. E., 1915. Victorian Hydroida with description of new species. *Geelong Naturalist* 6(3): 51–59, pls 7–9.

NUTTING, C. C., 1915. American hydroids. Section III. The Campanularidae and Bonneviellidae.—Smithsonian Institution. *Special Bulletin of the United States National Museum* 4(3): 1–126.

ÖSTMAN, C., 1987. New techniques and old problems in hydrozoan systematics. In *Modern trends in the systematics and evolution of hydroids and hydromedusae.* Jean Bouillon, Ferdinando Boero, Fabio Cicogna & Paul F. S. Cornelius, eds. Oxford Science Publications.

PENNYCUIK, P. R., 1959. Faunistic records from Queensland. Part 5—Marine and brackish water hydroids. *Papers of the Department of Zoology of the University of Queensland* 1: 141–210.

PHILBERT, M., 1935. Le phénomène de stolonisation chez trois espèces d'hydraires fixés sur les posidonies en Mediterranée. *Bulletin of the Oceanographic Institute, Monaco* 663: 1–8.

PICARD, J., 1952. Les hydrozoaires des herbiers de zostéracées des côtes françaises de la mediterranée. *Vie et Milieu* 2 (Suppl.): 217–223.

RAMIL, F. & VERVOORT, W., 1992. Report on the Hydroida collected by the 'Balgim' expedition in and around the Strait of Gibraltar. *Zoologische Verhandelingen* 277: 1–262.

RALPH, P. M., 1956. Variation in *Obelia geniculata* (Linnaeus, 1758) and *Silicularia bilabiata* (Coughtrey, 1875) (Hydroida, F. Campanulariidae). *Transactions of the Royal Society of New Zealand* 84: 279–296.

RALPH, P. M., 1957. New Zealand thecate hydroids. Part 1. Campanulariidae and Campanulinidae. *Transactions of the Royal Society of New Zealand* 34(4): 811–854.

RALPH, P. M., 1961. New Zealand thecate hydroids. 4. The family Plumulariidae. *Transactions of the Royal Society of New Zealand* 1(3) : 19–74.

REDIER, L., 1966. Hydraires et Bryozoaires. In *Contribution à l'étude des rivages coralliens d'après les récoltes de Yves Plessis, en Océanie (Mission Singer-Polignac). Cahiers de Pacifique* 9: 78–122, pls 1–3.

RITCHIE, J., 1909. Supplementary report on the hydroids of the Scottish National Antarctic Expedition. *Transactions of the Royal Society of Edinburgh* 47: 65–101.

RITCHIE, J., 1911. Scientific results of the trawling expedition of H.M.C.S. 'Thetis'. *Memoirs of the Australian Museum* 4(2): 807–869.

ROCA MARTINEZ, I., 1986. Estudio de los Cnidarios Bentonicos de las aguas costeras de Mallorca. Thesis, University de los Islas Baleares, Palma de Mallorca: 1–32, figs 1–18.

RUSSELL, F. S., 1953. *The medusae of the British Isles. Anthomedusae, Leptomedusae, Trachymedusae and Narcomedusae.* Cambridge University Press. 530 p.

RYLAND, J. S. & GIBBONS, M. J., 1991. Intertidal and shallow water hydroids from Fiji. 2. Plumulariidae and Aglaopheniidae. *Memoirs of the Queensland Museum* 30(3): 525–560.

SARS, M., 1851. Beretning om en i sommeren 1849 foretagen zoologisk reise i Lofoten og Finmarken. *Nytt Magasin for Naturvidenskapene* 6: 121–211.

SARS, M., 1869. In Sars, G. O., Bidrag til kundskaben om norges Hydroider. Forhandlinger i Videnskabs-Selskabet i Christiania 1873, p. 91–150.

SHEPHERD, S. A. & WATSON, J. E., 1970. The sublittoral ecology of West Island, South Australia: 2. The association between hydroids and algal substrate. *Proceedings of the Royal Society of South Australia* 94: 139–146.

SOUTHCOTT, R. V., 1982. Jellyfishes (Classes Scyphozoa and Hydrozoa). In *Marine invertebrates of southern Australia*. Part 1. S. A. Shepherd & I. M. Thomas, eds. Government Printer, South Australia. p. 115–159.

SPLETTSTÖSSER, W., 1929. Beiträge zur Kenntnis der Sertulariiden. *Thyroscyphus* Allman, *Cnidoscyphus* nov. gen., *Parascyphus* Ritchie. *Zoologische Jahrbücher* (System Abt.) 58: 1–134.

STECHOW, E., 1919. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete I. *Zoologische Jahrbücher* (Syst.) 42: 1–172.

STECHOW, E., 1923. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete II. *Zoologische Jahrbücher* (Syst.) 47: 1–270.

STECHOW, E., 1924. Diagnosen neuer Hydroiden aus Australien. *Zoologischer Anzeiger* 59: 57–69.

STECHOW, E., 1925. Hydroiden von West- und Sudwest-australien nach den Sammlungen von Prof. Dr Michaelsen und Prof. Dr Hartmeyer. *Zoologische Jahrbücher* (Syst.) 50: 191–269.

STRANKS, T. N., 1993. Catalogue of recent cnidarian types. *Occasional Papers from the Museum of Victoria* 6: 1–26.

UCHIDA, T., 1938. Medusae in Onagawa Bay and its vicinity. *Science Reports of the Tohoku University* 13(4): 47–58.

VANHÖFFEN, E., 1910. Die Hydroiden der Deutschen Südpolar-expedition 1901–1903. *Deutsche Südpolar-Expedition 1901–1903* 9 Zoologie 3: 271–340.

VERVOORT, W., 1941. Biological results of the Snellius Expedition. XI. The Hydroida of the Snellius Expedition (Milleporidae and Stylasteridae excluded). *Temminckia* 6: 186–240.

VERVOORT, W., 1959. The Hydroida of the tropical west coast of Africa. *Atlantide Report* 5: 211–325.

WATSON, J. E., 1973. Pearson Island expedition 1969 — 9. Hydroids. *Transaction of the Royal Society of South Australia* 97(3): 153–200.

WATSON, J. E., 1978. New species and new records of Australian athecate hydroids. *Proceedings of the Royal Society of Victoria* 90(2): 301–314.

WATSON, J. E., 1985. The genus *Eudendrium* (Hydrozoa: Hydroida) from Australia. *Proceedings of the Royal Society of Victoria* 97(4): 179–221.

WATSON, J. E., 1992. The hydroid community of *Amphibolis* seagrasses in south-eastern and south-western Australia. In *Aspects of hydrozoan biology*, J. Bouillon, F. Bocro, F. Cicogna, J. M. Gili & R. G. Hughes, eds, *Scientia Marina* 56(2–3): 217–227.

PROCEEDINGS

OF THE

ROYAL SOCIETY OF VICTORIA

INCLUDING

TRANSACTIONS OF MEETINGS

Volume 107

CONTENTS OF VOLUME 107

GRANITIC REGOLITH AND LANDSCAPE EVOLUTION OF WILSONS PROMONTORY, VICTORIA

S. M. Hill* & E. B. Joyce

School of Earth Sciences, The University of Melbourne, Parkville, Victoria 3052
*Present address: The Centre for Australian Regolith Studies, The Australian National University, Canberra, ACT 0200

Hill, S. M. & Joyce, E. B., 1995:07:31. Granitic regolith and landscape evolution of Wilsons Promontory, Victoria. *Proceedings of the Royal Society of Victoria* 107 (1): 1–10. ISSN 0035-9211.

The granitic regolith and associated landscape features at Wilsons Promontory have evolved from a major period of deep weathering that occurred since the Devonian, probably after the widespread Permian glacial erosion. During these times of relative tectonic stability and subdued topography, conditions were conducive to the accumulation of weathering products in deep profiles with minimal erosion of this material. Topographic relief and tor morphology considerations suggest the existence of a single weathering profile at least 300 m deep. Tectonic instability since the mid Cretaceous led to faulting and associated uplift of much of the Wilsons Promontory area, instigating the stripping of the deep weathering profiles. The progressive stripping of the deep weathering profile is reflected in the derived sedimentary record. Remnants of deep weathering profiles and related palaeosurfaces are found in areas where the influence of erosion has been limited, such as in downfaulted areas in the interior of the highland ridges. Mobilisation of regolith materials in the Late Cenozoic has occurred in debris flows and outwash fans which now mantle many of the lower slopes and adjacent lowlands. Marginal marine and aeolian sand deposition, largely derived from the granitic weathering products, has occurred during the Late Cenozoic.

SINCE the nineteenth century Wilsons Promontory has attracted investigators from many of the branches of natural science, in particular the biological and earth sciences. Geologists have mostly focused on aspects of the Cenozoic sedimentation (e.g. Tuddenham 1970; Oyston 1988) or the geological features associated with the igneous petrology of the Devonian Wilsons Promontory Batholith (e.g. Wallis 1980, 1981, 1988; Carson 1990). None of these studies has made a detailed examination of the landscape evolution which is the topic of this paper.

Wilsons Promontory, the most southerly point of the Australian mainland, lies approximately 230 kilometres southeast of Melbourne, Victoria. Most of Wilsons Promontory and adjacent islands are located within Wilsons Promontory National Park and Commonwealth land associated with the lighthouses at South East Point, and Citadel Island in the Glennie Group (Fig. 1).

GEOLOGICAL SETTING

Wilsons Promontory consists of granite from a high level, composite body of S-type intrusives (Wallis 1981, 1988). Richards & Singleton (1981) showed the batholith to be Late Devonian, with a K-Ar age of 379 ± 15 Ma. Wallis (1980, 1981, 1988) distinguished seven main granitic members based on differences in modal mineralogy, bulk rock geochemistry and textural characteristics. The most distinctive differences between the members are in the modal percentages of K-feldspar, plagioclase and biotite. The Promontory Leucogranite (>38% K-feldspare, <17% plagioclase and <5% biotite) and the Xenolith Biotite Adamellite (<30% K-feldspar, >25% plagioclase and >12% biotite) represent the compositional extremes. The internal geometry of the batholith is dominated by shallow (0–40°) easterly diping sheet-like granitic bodies which outcrop as elongate NNW–SSE trending zones (Wallis 1981, 1988).

The country rocks intruded by the Wilsons Promontory Batholith are Late Ordovician (Gisbornian) tightly folded sandstones and shales, as can be seen at the intrusive contact at Red Bluff near Yanakie. The batholith is flanked by Mesozoic and Cainozoic sediments of the Gippsland and Bass Basins. The sediments and tectonic structures within these basins relate to the continental rifting of Gondwana (Etheridge 1988; Duddy & Green 1992), when Australia was separated from Antarctica to the south and the Lord Howe Rise—New Zealand to the east.

Cenozoic sedimentary deposits within the area include Late Pliocene—Pleistocene terrestrial gravels equivalent to the Haunted Hills Formation (Hocking 1988). These ocur in the Corner Inlet area where they consist of ferruginous, well-rounded pebbles of quartz, chert and sandstone

(Oyston 1988). Marginal marine and aeolian sand deposits in the lowlands and along the coastal margins of Wilsons Promontory range from the Late Pliocene to the present (Tuddenham 1970; Oyston 1988). Active coastal sedimentation at Wilsons Promontory is characterised by the deposition of siliceous sands along the east coast and calcareous sands along the west coast. The calcareous sands are derived from submarine calcareous ridges to the west (Tuddenham 1970). Old siliceous sands in areas of the west coast (such as at Leonard Bay and Little Oberon Bay) represent sedimentation that occurred before the Yanakie Isthmus was developed and became a barrier to the movement of further siliceous sands from the east (Oyston 1988).

Fig. 1. Location map of the Wilsons Promontory area showing some of the sites mentioned in the text.

GENERAL GEOMORPHIC SETTING

Wilsons Promontory consists of a series of ridges of granitic highlands with adjacent low-lying areas of Cenozoic sediments. A major granitic ridge runs approximately north–south along the centre of the Promontory. This ridge contains the major peaks of Wilsons Promontory: Mt Boulder, Mt Wilson, Mt Ramsay, Mt Vereker and the highest peak Mt Latrobe (754 m). These major peaks are separated by a series of saddles. A major pass occurs between Mt Wilson and Mt Boulder, where an east–west trending valley runs the width of the Promontory between Oberon and Waterloo Bays. Branching from this central highland area are a series of smaller east–west ridges which terminate as prominent coastal headlands. The intervening bays and coves represent submerged valleys and lowlands.

The northeastern part of Wilsons Promontory consists of another north–south trending granitic ridge, forming the core of the Singapore Peninsula. This ridge contains the peaks of Mt Singapore, Mt Margaret and Mt Roundback, and rises to 347 m at Mt Hunter. A low east–west trending ridge connects the main highland ridge and the ridge of the Singapore Peninsula, between Sugar Basin Swamp and St Kilda Junction (Fig. 1). A mostly submarine north–south trending granitic ridge also occurs approximately five kilometres off the west coast of Wilsons Promontory. Exposures of parts of this ridge from north–south trending elongate islands such as within the Glennie Group.

In many areas the granitic highlands abut sandy lowlands consisting of outwash from the granitic highlands and associated aeolian and marine deposits. A low sandy area with large transgressive dune systems, known as the Yanakie Isthmus, joins the northwestern part of Wilsons Promontory to the mainland (Fig. 1).

THE GRANITIC REGOLITH MATERIALS

'Granitic regolith' here refers to all of the weathering products and associated transported material derived from the granite rocks. The weathered material which still retains the structures of the original rock is termed saprolite. In the upper levels of the weathering profile this material becomes disrupted, constituting what is termed the mobile zone. Fig. 2 shows some of the typical features of granitic regolith profiles. The granitic regolith materials at Wilsons Promontory can be subdivided into two major categories: in situ granitic weathering material (or saprolite and corestones)

Fig. 2. Characteristic features and zones of a typical deep granitic weathering profile (after Ollier 1984).

and granitic material (both fresh and weathered) which has been mobilised downslope.

In situ granitic weathering material

The in situ material consists of saprolite often containing corestones of fresh granite, which may form tors as a result of erosion of the softer saprolite.

X-ray diffraction, Scanning Electron Microscope and thin section investigations (Hill 1992) reveal the mineral composition of the saprolite to be dominated by secondary minerals (particularly kaolinite, mostly derived from feldspar alteration) and resistant minerals (particularly quartz and minor tourmaline). Corestones may be of both the angular and rounded type depending mainly upon their relationship to zones within the weathering profile (Fig. 3).

Areas of in situ weathering material are mostly restricted to the interior of the central highland area where they have been protected from the

Fig. 3. Exposed section through the Little Oberon Bay debris fans looking south along coastal cliffs at southern end of Little Oberon Bay Beach (north end of Oberon Bay). Note the large boulders of fresh granite at the base of the cliffs which have been transported by the debris flows.

influence of erosive stripping. Some of the best exposures of in situ weathered granite can be seen in cuttings along the Wilsons Promontory Road and Mt Oberon Road and in the quarry on the lower slopes of Mt Oberon (Hill 1992). Stripping of much of this material from westerly and southerly exposures has been due to their exposure to the prevailing direction of wind, rain and coastal swells. These agents directly contribute to stripping as well as indirectly contributing as a result of their influence on vegetation. Exposures of fresh granite occur where stripping has been complete, such as on prominent coastal headlands.

Mobilised granitic material

Slope deposits due to the downslope movement of granitic weathering products consist of a mixture of unconsolidated gravels, sands and clays, with fragments of fresh and weathered granite. They are found flanking the granitic highlands and extending into adjacent valley systems and lowlands. The extensive development of slope deposits at Wilsons Promontory is due to a combination of the steep and dissected terrain, an abundance of weathered material with reduced bulk density and shear strength, a tendency for the area to experience periods of torrential rain, and the susceptibility to removal of the vegetation cover by forest fires (Hill 1992).

Coastal exposures of the slope deposits that mantle the western slopes of Mt Oberon and extend into Little Oberon Bay reveal the internal organisation of these features (Fig. 3). Sorting within the deposits is poor and the structure is generally chaotic but in some parts is sub-horizontally bedded sands and gravels. Particle sizes range from clay, silt, sand and gravel size particles to granitic boulders over 10 m in diameter (see Fig. 3). The large boulders are matrix-supported in a framework of silt and clay size particles.

The features of much of these sections are typical of debris flows (Coates 1977; Selley 1988), where the large boulders would have been effectively transported large distances by being supported by the high strength of the matrix. The subhorizontal bedded and channelled units represent periods of fluvial transport, such as in ephemeral stream or sheet flood events. Similar deposits have also been described from other granitic regions throughout the world (e.g. Ruxton & Berry's 1957 work in Hong Kong). The dense colonisation of vegetation, development of pedogenic features, stratigraphic relationship with overlying siliceous sand, and the grading of the fans to a lower sea level

indicate that these deposits are no longer active and are probably of Pleistocene age. Similar slope mobilisation, however, still occurs to the present day elsewhere on Wilsons Promontory. This can be seen at the southern end of Waterloo Bay where an approximately 250 m long slope has recently been cleared by a recent debris torrent, and also along sections of the Wilsons Promontory Road south of Darby River.

GEOMORPHIC FEATURES

Drainage and lineaments

A notable feature of the drainage system at Wilsons Promontory is the pronounced linear trend of most of the stream courses (Fig. 4). This type of pattern is typical of granitic areas and reflects joint and fault structures within the granitic bedrock (Hills 1975). Weathering and erosion have been concentrated along many of these structures, resulting in their expression as linear valleys. In some areas of the granitic highlands (such as
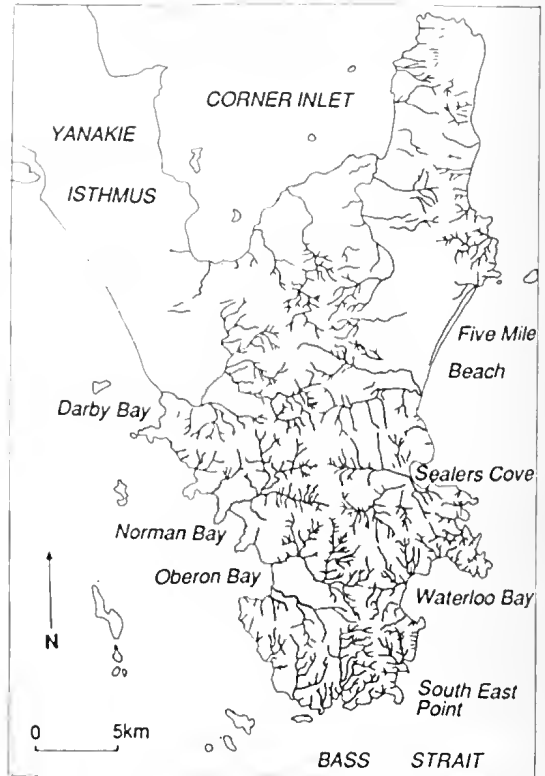
Fig. 4.   The drainage system of Wilsons Promontory.

within the Vereker Range) streams have more of a dendritic pattern (Fig. 4). This is considered to be due to deep saprolitic covers which serve to reduce the influence of structures .

Wallis (1981) and Hill (1992) mapped some of the major lineaments in the Wilsons Promontory area (Fig. 5). Fault movements are shown by the displacements of earlier structures and the intrusive sheets of the batholith (Wallis 1981). These movements have also displaced an earlier formed palaeoplain as well as the associated regularly arranged weathering zones. Fault movement has been active from the Cretaceous to the present (Etheridge 1988).

Major northeast–southwest lineaments within the batholith are related to the Early Cretaceous transfer faults of the Bass Basin (Etheridge et al. 1985). Vertical movements along these faults, since the early Cretaceous to the late Tertiary, appear to be responsible for the down-throwing of the Corner Inlet–Yanakie Isthmus area to the north and the area offshore to the south-southeast of Wilsons Promontory.

North–south trending faults also appear to have facilitated major vertical movements, in particular along the Jennings Fault west of the Glennie Group of islands (Fig. 5), and along lineaments within the southern and central parts of the main granitic highlands, where upthrown blocks form prominent peaks such as the Boulder Range and Mts Norgate, Wilson, Ramsay and Latrobe (Fig. 7). The development of the valley associated with the north–south Roaring Meg Lineament has diverted an earlier east–west drainage system and deflected it to the south (Fig. 4). These faults are probably related to Cretaceous and Cenozoic reactivation of older Palaeozoic structures.

Palaeosurfaces

Within the steeply sloping and dissected highlands of Wilsons Promontory are high areas of flat to
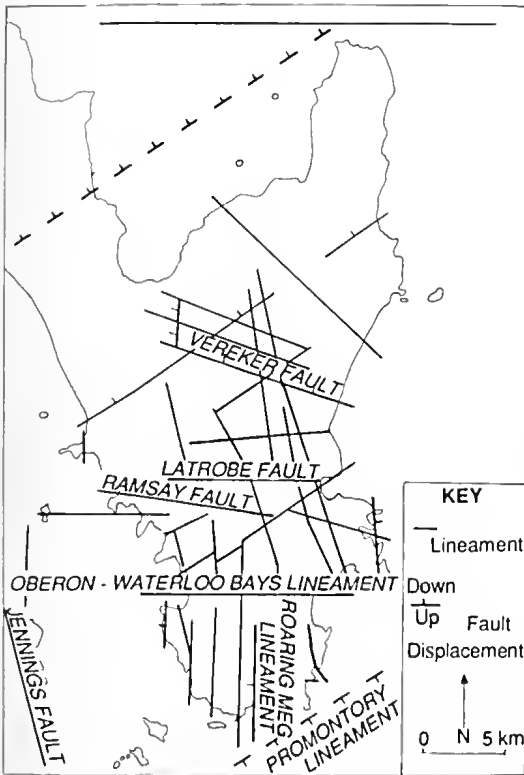
Fig. 5. Major lineaments of Wilsons Promontory, derived from air photograph interpretation field survey and Wallis (1981).
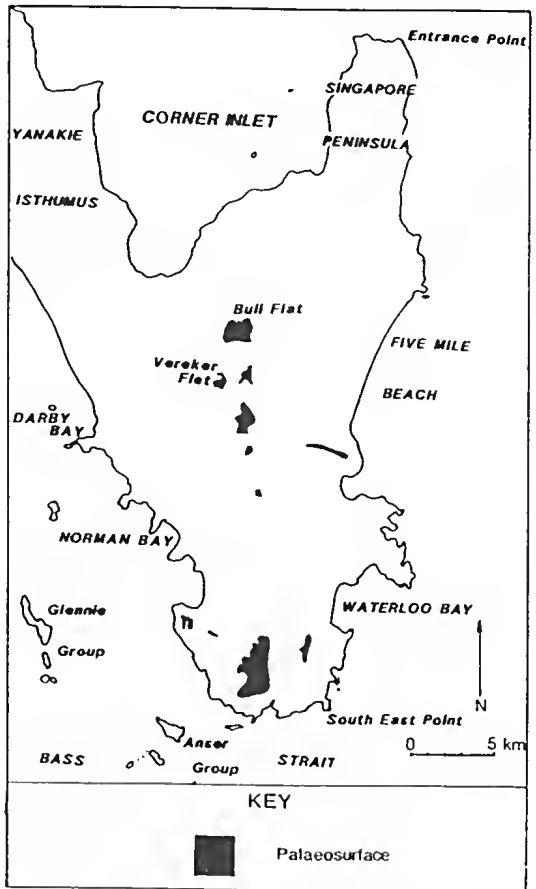
Fig. 6. Palaeosurface distribution at Wilsons Promontory. These areas are characterised by flat to slight slope gradients and deep saprolitic weathering profiles.

slight slopes underlain by saprolite. These features are derived from an ancient landsurface (palaeosurface) that has been preserved in the present landscape. They are mostly confined to the central, inland areas of Wilsons Promontory, or are sheltered between topographic high points (Fig. 6). Erosion has been restricted in these residual areas and allowed the preservation of the surfaces and their deep weathering profiles. In more exposed areas, such as along the coast and at the margins of uplifted fault blocks, much of this deep regolith has been stripped exposing fresh granite.

Major differences in elevation (up to 400 metres) occur between the palaeosurface remnants (Fig. 6). The differences in elevation between localised areas of concordant elevation occurs along the major lineaments shown in Fig. 5. Faulting has apparently displaced a landsurface of lower relief. This palaeosurface has been uplifted most within the central highland area, around Mt Ramsay and Mt Vereker (Figs 6 and 7). The northern part of the batholith between the Yanakie Isthmus and the Singapore Peninsula has subsided relative to these highlands during the formation of the Corner Inlet Basin. Much of this movement appears to have occurred along the Vereker Fault, where cliffs of fresh granite at the northern end of the Vereker Range represents the faultline escarpment. The deeply weathered, subdued terrain to the north of this fault may be associated with a down-faulted part of the ancient palaeosurface.

Tors

Residual boulders of granite, known as tors, are a common landform feature of granitic terrains. They are derived from the stripping of saprolite from weathering zones containing rounded and angular corestones.

A traverse along the centre of the northern spur of Mt Boulder, in the south of Wilsons Promontory, demonstrates a general decrease in tor size and angularity with an increase in altitude (Fig. 8). The lengths of the intermediate axes of 339 tors encountered along a 1500 m long and 50 m wide transect have been plotted against the altitude of the specific tors, determined from a 1:25 000 scale topographic map (Fig. 8A). This is an ideal location to study this relationship because variables that may influence tor morphology (such as the petrographic character of the parent rock, joint pattern and slope mobilisation of tors) are negligible or easily identifiable (Hill 1992). For instance, the slight decreases in tor size trend at 170 and 230 metres above sea level may be accounted for by small zones of closer joint spacing.

The general decrease in tor size and angularity associated with an increase in altitude conforms to the trend found in typical granitic weathering profiles, where the upper portions of the profile contain progressively more weathered corestones which are smaller and more rounded (Fig. 2). The
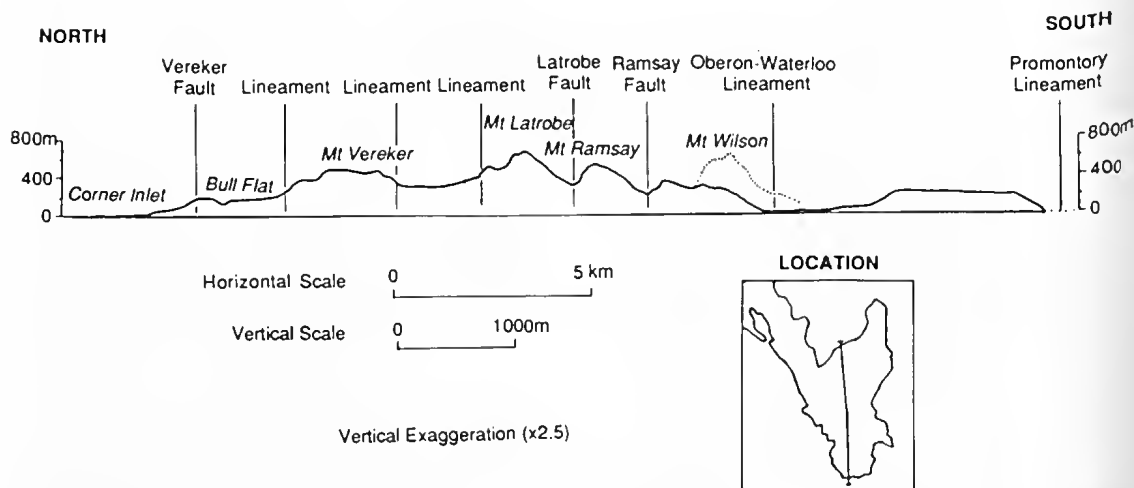
Fig. 7. A north–south cross section across the centre of Wilsons Promontory, with location of major faults and lineaments associated with areas of uplift and subsidence as well as vertical displacement of palaeosurfaces.
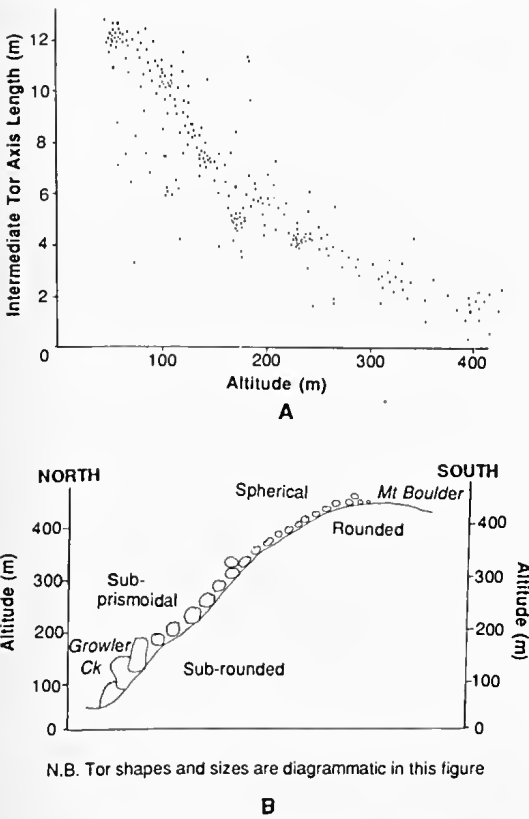
Fig. 8. Tor features of Mt Boulder, Wilsons Promontory. A. Plotted relationship between intermediate tor axis length and altitude, showing a significant inverse relationship. B. Diagrammatic representation of changes in tor shape with altitude.

occurrence of this relationship between 100 and 400 metres above sea level can therefore be related to the regular arrangement of weathering zones within an extensive, single, stripped weathering profile, that was in excess of 300 m deep.

DISCUSSION:
THE DEPTH AND AGE OF WEATHERING

Deep weathering has been a major influence on the landscape evolution of Wilsons Promontory, causing the formation of the granitic regolith materials, as well as many of the associated land-forms. Much of the original material has been removed by erosion, making it difficult to assess the extent and age of weathering. The evidence derived from this and previous studies will be discussed here.

Depth of weathering

In many granitic terrain models the surface relief is considered to be a reflection of the depth of stripping of an older deep weathering profile (Linton 1955; Ollier 1983). Stripping of deep weathering profiles in this area has been the major contributor to the development of relief in this area. Analysis of tor morphology suggests weathering in some areas reached depths of at least 300 m. This depth would have varied across the batholith, with even greater depths expected in major joint zones, possibly even approaching the order of the 800 m of relief now found at Wilsons Promontory. There has however been an additional contribution to the relief by tectonic activity. Differential vertical movements of fault blocks has been in the order of hundreds of meters, partly accounting for the relief within the Wilsons Promontory Batholith.

It is interesting to note that no areas of asso-ciated extrusive rocks or roof pendant country rock have been found within the batholith. Wallis (1981) considers that the batholith was emplaced at high levels of approximately 1–2 kilometres, with microgranites containing miarolitic cavities which now cap the summits of many peaks representing the near roof zone of the batholith. If this is the case then the overlying 1–2 kilometres of material has been eroded from above the batholith since the Late Devonian. It is likely that much of this material was eroded during the late Palaeozoic, particularly during the Permian when much of this region was covered by large ice sheets (Ollier 1977; Bowen & Thomas 1988). The timing of this erosion is considered further in the following discussion.

The age of weathering

Weathering of the Wilsons Promontory Batholith has occurred during its entire history of exposure to the near surface environment. The development of deep weathering profiles however has depended on periods when the weathering of the bedrock has predominated over the removal of the weathering profile by erosion.

The deep weathering and associated low relief palaeosurfaces most probably post-date Permian glaciation. Further evidence from this region supports this suggestion. Apatite Fission Track Analyses of granites from the Wilsons Promontory Batholith suggest relative tectonic stability between the Permian and mid Cretaceous, followed by uplift and erosion associated with the unconformity at the top of the Early Cretaceous Strzelecki Group within the Gippsland Basin (Duddy & Green 1992).

During this Mesozoic tectonic stability, conditions would have been suitable for the development of deep weathering profiles, as was the case in many other parts of southeastern Australia (Hills 1975; Jenkins 1988; Bird & Chivas 1989).

The onset of erosion in the mid Cretaceous is recorded in the sedimentary record in the Gippsland Basin, where there is a transition from the volcaniclastic Strzelecki Group to the detrital Latrobe Group. The Late Cretaceous to Oligocene Latrobe Group sediments represent terrigenous material derived from the margins of the Gippsland Basin, such as Wilsons Promontory (Lowry & Longley 1991). The dominance of quartz in these sediments is largely due to stripping of deeply weathered granites, such as at Wilsons Promontory, where there has been a relative accumulation of these stable minerals. Further evidence for Tertiary stripping of a deeply weathered terrain is shown by Eocene gravels in the Toora region north of Wilsons Promontory. These sediments contain an abundance of resistant minerals such as quartz, tourmaline and cassiterite, derived from the Wilsons Promontory granites (Spencer-Jones 1955). Labile minerals and clasts of fresh granite are absent from the sediments derived from the batholith area until late in the Cenozoic when they are included in slope deposits and Quaternary sands (Hill 1992). The sedimentation since the mid Cretaceous and through the Cenozoic therefore represents the progressive stripping of a deep weathering profile. Earlier derived sediments represent saprolitic materials with later contributions coming from less weathered zones in the profile as stripping extended to these depths.

The period before the mid Cretaceous is therefore likely to have been associated with the development of deep weathering profiles, and so the associated palaeosurfaces on which the profiles developed must be older. This palaeosurface is probably related to the Trias–Jura palaeoplain described by Hills (1975) in southeastern Australia. The onlapping of early Cretaceous Strzelecki Group sediments over granitic unconformity surfaces offshore of Wilsons Promontory and further west at Cape Woolami on Phillip Island adds further supports this age of the paleaosurface in this region. Tectonic instability since the mid Cretaceous has led to an increase in erosion, with the stripping of the deep weathering profiles in all but some central or protected areas within the main highlands. Further weathering of the granites would no doubt have occurred through the Tertiary to the present, but this is of less significance than the high rate of erosion that has occurred during these times. The minor Cenozoic weathering is

Represented by the profiles developed on the Cretaceous Strzelecki Group volcanoclastics within the South Gippsland Highlands to the north of Wilsons Promontory.

SUMMARY

The stages of landscape evolution

1. Deep weathering, probably during the Mesozoic, after the widespread glacial erosion during the Permian. The dominance of deep weathering versus erosion would have been facilitated by a relatively stable landscape of subdued relief.

2. Faulting and uplift of the Wilsons Promontory Batholith in the mid Cretaceous resulted in erosion of the deep weathering profiles. The eroded weathered material was transported into the Gippsland Basin and contributed to the detrital Latrobe Group sediments.

3. Predominance of erosive stripping of the granitic regolith in the mid to late Tertiary with a minor continuation of weathering. Stripping, particularly of upthrown blocks, occurred by stream dissection with downslope movement of regolith, on fault blocks. Deep regolith profiles remain in areas with greater preservation potential such as downthrown blocks.

4. Late Cenozoic deposition of quartz sands, largely derived from granite regolith material, around the coastal margins of the batholith. The Yanakie Isthmus formed as a tombolo, joining the granitic highlands to the mainland.

5. Deposition of calcareous sands derived from carbonate reefs to the west, during the Pleistocene and Holocene. These sands have been reworked into large easterly transgressing dunes since the Pleistocene.

6. Continued stripping of granitic regolith to the present, particularly along coastal margins, with less significant weathering. Deposition of siliceous sands along the east coast and calcareous sands along the west coast. Alluvial outwash and swamp deposition in low lying areas.

CONCLUSIONS

Wilsons Promontory is an area of Devonian granite. The evolution of the present Wilsons Promontory landscape began after the granite was exposed, presumably by the glacial erosion of the Permian. Since that time the granites of the Wilsons Promontory Batholith have been exposed to near surface conditions where they have been deeply weathered. In the Mesozoic a palaeoplain existed

and weathering predominated over erosion. The resulting deep weathering profiles extended to depths in excess of 300 metres. Tectonic instability in the early Cretaceous instigated stripping of the deep weathering profiles, contributing sedimentary material to adjacent areas such as the Gippsland Basin. Remnants of the deep weathering profiles that began their development during the Mesozoic owe their present survival to areas where the influence of erosion has been limited, such as down-faulted blocks and the interior and sheltered parts of the highland areas.

ACKNOWLEDGEMENTS

REFERENCES

BIRD, M. I. & CHIVAS, A. R., 1989. Stable-isotope geochronology of the Australian regolith. *Geochimica et Cosmochimica Acta* 53: 3239–3256.

BOWEN, R. L. & THOMAS, G. A., 1988. Permian. In *Geology of Victoria*. J. R. Douglas & J. A. Ferguson, eds, Geological Society of Australia, Victorian Division, 195–212.

CARSON, C. J., 1990. Microgranite enclaves and the petrogenesis of the Wilsons Promontory Batholith, Southern Victoria. BSc (Hons) Thesis, Department of Geology, Monash University, Unpublished.

COATES, D. R., 1977. Landslide Perspectives. *Geological Society of America, Reviews in Engineering Geology* 3: 3–28.

DUDDY, I. R. & GREEN, P. F., 1992. Tectonic development of the Gippsland Basin and environs: Identification of key episodes using Apatite Fission Track Analysis (AFTA). *Gippsland Basin Symposium*, 111–120.

ETHERIDGE, M. A., 1988. Bassian Zone. In *Geology of Victoria*. J. G. Douglas & J. A. Ferguson,

eds. Geological Society of Australia, Victorian Division, 26–28.

ETHERIDGE, M. A., BRANSON, J. C. & STUART-SMITH, P. G., 1985. Extensional basin-forming structures in Bass Strait and their importance for hydrocarbon exploration. *The APEA Journal* 25(1): 344–361.

HILL, S. M., 1992. The granitic regolith and associated geomorphology of Wilsons Promontory, Victoria, Australia. BSc (Hons) Report, School of Earth Sciences, The University of Melbourne, 66 p. plus references, appendices and maps. Unpublished.

HILLS, E. S., 1975. *The Physiography of Victoria* (5th Edition). Whitcombe and Toombs, Melbourne.

HOCKING, J. B., 1988. Gippsland Basin. In *Geology of Victoria*. J. G. Douglas & J. A. Ferguson, eds, Geological Society of Australia, Victorian Division, 322–347.

JENKIN, J. J., 1988. Geomorphology. In *Geology of Victoria*. J. G. Douglas & J. A. Ferguson, eds, Geological Society of Australia, Victorian Division, 403–419.

LINTON, D. L., 1955. The Problem of Tors. *Geographical Journal* 121: 470–487.

LOWRY, D. C. & LONGLEY, I. M., 1991. A new model for the Mid-Cretaceous structural history of the northern Gippsland Basin. *The APEA Journal* 31: 143–153.

OLLIER, C. D., 1977. Early landform evolution. In *Australia, a Geography*. D. N. Jeans, ed., Sydney University Press, Sydney, 85–98.

OLLIER, C. D., 1983. Geomorphology and weathering in Australia and its relevance to geochemical exploration. In *Geochemical Exploration, Workshop Course 232/83*, A. S. Joyce & I. Nichol, eds, Australian Mineral Foundation, 172–89.

OLLIER, C. D., 1984. *Weathering* (2nd Edition). Longman Inc., New York, 270 p.

OYSTON, B., 1988. The geology and Cainozoic evolution of the Yanakie Isthmus, Victoria. BSc (Hons) Thesis, Department of Geology, The University of Melbourne, Unpublished.

RICHARDS, J. R. & SINGLETON, O. P., 1981. Palaeozoic Victoria, Australia: Igneous rocks ages and their interpretation. *Journal of the Geological Society of Australia* 28: 395–421.

RUXTON, B. P. & BERRY, L., 1957. The weathering of granite and associated erosional features in Hong Kong. *Bulletin of the Geological Society of America* 68: 1263–1292.

SELLEY, R. C., 1988. *Applied Sedimentology*. Academic Press, London.

SPENCER-JONES, D., 1955. Geology of the Toora Tin Field. *Bulletin 54, Geological Survey of Victoria.*

TUDDENHAM, W. G., 1970. The coastal geomorphology of Wilsons Promontory, Victoria: Implications concerning Quaternary sedimentation around the shores of Bass Strait. MSc Thesis, Department of Geography, Sydney University, Unpublished.

WALLIS, G. L., 1980. Wilsons Promontory: An introduction to its geology. *Victorian Naturalist* 97: 194–199.

WALLIS, G. L., 1981. The Geology of the Wilsons Promontory Batholith, Victoria: A study of the composition, emplacement and structure of an S-type granitoid. MSc Thesis, Department of Geology, Monash University, Unpublished.

WALLIS, G. L., 1988. Wilsons Promontory. In *The Victorian Geology Excursion Guide*. 1. Clark & B. Cook, eds, Australian Academy of Science, Canberra, 353–372.

TERRESTRIAL MAMMALS IN VICTORIA—A HISTORY OF DISCOVERY

J. H. Seebeck

Department of Conservation and Natural Resources, Flora and Fauna Branch, 123 Brown Street, Heidelberg, Victoria 3084

The history of discovery of non-marine mammals in Victoria by Europeans is traced by reference to literature and museum records. Three phases of discovery and documentation are recognised. Before the establishment of the National Museum of Victoria (now Museum of Victoria) in 1854, most records are literature-based, although some specimens were sent to European museums. After 1854, the formal collection and curation of natural history material, coupled with organised collecting expeditions, set the scene for official checklists of species to be prepared. Modern understanding of distribution, habitat use and ecology have been used to synthesise as complete a record as possible and to clarify some questionable identities of species present.

THE MOST recent list of mammals recorded for Victoria (DCE 1991) includes 112 non-marine species, of which 91 are native. Seventy-one of these are still extant in the State. The distribution of all species is increasingly being documented in the Atlas of Victorian Wildlife (Menkhorst 1987a) and an understanding of status and conservation prospects also continues to grow. However, this understanding has been almost 200 years in the making. This paper traces the development of knowledge about the species of native terrestrial mammals that were present in Victoria at the time of European contact.

METHODS

The information presented is largely derived from literature surveys and from examination of records held at the Museum of Victoria.

I have searched the entries in Ferguson's Bibliography (1941–69) to direct my investigations to relevant works published before the establishment of the Museum of Victoria in 1854, when formal documentation of the State's fauna began.

Current knowledge of the distribution (Atlas of Victorian Wildlife database), habitat and ecology of Victoria's mammals has been used to identify the species in some early reports.

I have used the modern vernacular names accepted by the Australian Mammal Society and the Department of Conservation and Natural Resources, Victoria.

RECORDS BEFORE 1854

The first report of non-marine mammal from what is now Victoria was that of George Bass, who, in January 1798, discovered and explored Western Port. He noted that, during his 12 days there, he saw 'a few of the brush kangaroo, the wallabah, but no other kind' (Rawson 1946). Three species

of wallaby may have occurred in the region—the Black Wallaby, *Wallabia bicolor*, which is still extant on Phillip Island and the adjoining mainland; the Red-kneeked Wallaby, *Macropus rufogriseus*, for which there are no formal records but for which habitat was suitable at Western Port (the nearest population is at Rosedale in South Gippsland); and the Red-bellied Pademelon, *Thylogale billardierii*, which is now extinct in Victoria. Although none of these species had been formally named at that time, Bass would have been familiar with *W. bicolor* and *M. rufogriseus*—the latter is still widely known at the Brush Wallaby. However, it is not now possible to identify with certainty the species (and there may well have been more than one) seen by Bass.

The *Sydney Cove* was wrecked on Preservation Island in Bass Strait in 1797. The survivors set out for Sydney but their boat was wrecked on the Victorian coast 12 days later. They then attempted to walk to Sydney (Rawson 1946). Barker & Caughley (1992) noted that the survivors obtained a kangaroo tail from aborigines, and suggested that this took place in Victoria. I have calculated the distance travelled by the party, and the event must have occurred on the New South Wales south coast—they had walked some 270 miles (340 km) by their reckoning from their starting point near Cape Everard (50 km from the New South Wales/Victorian border) by that time.

Lieutenant James Grant explored Western Port in March 1801, and on Churchill Island found 'burrows' which he 'supposed to be those of the bandicoot rat' (the Southern Brown Bandicoot, *Isoodon obesulus* is common around Western Port, though there are no modern records from any of the islands). He also saw kangaroo and Dingo (*Canis familiaris*) tracks, and one of his dogs was attacked by an unknown animal (Grant 1803). Nearly a year later, Lieutenant John Murray

was at Western Port, and in February 1802 discovered Port Phillip Bay. Apart from recording that the natives wore possum skin cloaks he made no mention of land mammals in his journal (Lee 1915).

Even Matthew Flinders, hard on the heels of Murray into Port Phillip, only recorded seeing a 'kangaroo' (probably the Eastern Grey Kangaroo, *Macropus giganteus*) near the foot of the You Yangs during his explorations in May 1802 (Flinders 1814). The botanist with Flinders, Robert Brown, recorded a Dingo, as well as tracks and droppings of kangaroos, and noted that the natives wore kangaroo skin cloaks (Willis & Skewes 1955). Peter Good, the gardener on Flinders' ship 'Investigator' also saw tracks of both Dingo and kangaroo (Austin 1974).

The next visitors to Port Phillip, in January 1803, were Lieutenant Charles Robbins and party, which included Charles Grimes, the Surveyor-General, and James Flemming, a gardener. Their account contains no records of land mammals, despite providing a detailed record of the appearance of the countryside (Shillinglaw 1879).

Two accounts of the short-lived settlement at what is now Sullivans Bay, near Sorrento, in 1803–04 provide records of mammals. The Reverend Robert Knopwood recorded the measurements of a male *M. giganteus* which formed the main course for dinner on 14 November 1803 (Shillinglaw 1879). James Tuckey (1805) commented on the natives' use of possums (Common Brushtail Possum, *Trichosurus vulpecula*) and kangaroos, and listed kangaroos (in 'considerable numbers'), native dog, opossum, flying squirrel (Sugar Glider, *Petaurus breviceps*) and 'field-rat' – probably the Swamp Rat *Rattus lutreolus*. The Bush Rat, *R. fuscipes*, is not recorded for the Mornington Peninsula (Atlas of Victorian Wildlife).

William Buckley lived with aborigines around the Geelong–Otway area for 27 years, between 1808 and 1835. An account of his life during those years was published in 1852 (Morgan 1852). Buckley reported hunting and eating a number of native mammal species, but it is not possible to date the records precisely. Included in his diet, and sometimes also used for skins for clothing, were kangaroo (Eastern Grey Kangaroo, but may also have included Black Wallaby and Red-necked Wallaby), possum (Common Brushtail Possum), Dingo, Fur Seal (*Arctocephalus pusillus*), kangaroo-rat (possibly Long-nosed Potoroo, *Potorous tridactylus*, but may have also been Tasmanian Bettong, *Bettongia gaimardi*), 'squirrels' (Sugar Glider, *Petaurus breviceps* or Yellow-bellied Glider, *Petaurus australis*), Koala (*Phascolarctos cinereus*),

Wombat (Common Wombat, *Vombatus ursinus*), rats and mice (Bush Rat, *Rattus fuscipes* and Swamp Rat, *Rattus lutreolus*, are both present in the area, as are several species of *Antechinus* and at least one of *Sminthopsis*, all of which are often called 'Marsupial Mice').

During Hume and Hovell's journey to Port Phillip in 1924–25, Bland (1831) recorded kangaroos and wombats (Common Wombat). Hovell's journal of his second visit to the Port Phillip District, in 1826–27 (Hibbins 1984) records the hunting of kangaroos with dogs, and the use of kangaroo meat and skins by aborigines on the northern part of the Mornington Peninsula. Kangaroos were 'plentiful' around the 1826–28 settlement at Corinella, in Western Port (Weathcrall 1826).

Settlement (and exploration) of Victoria really began in 1834, and accounts by settlers and explorers during the mid to late 1830s record some encounters with native mammals. Edward Henty set his dogs onto kangaroos (probably the Eastern Grey Kangaroo, but may have included the Western Grey Kangaroo, *Macropus fuliginosus*) early in December 1834, and Dingoes were a continuing problem to his flocks of sheep in south-western Victoria (Bassett 1954). Henty also reported that kangaroos were 'getting thin, being much hunted'. He also was probably the first person to introduce Rabbits, *Oryctolagus cuniculus*, to Victoria, four being landed at Portland on 19 December 1834, from Launceston (Learmonth 1934).

Joseph Hawdon overlanded cattle from New South Wales to Adelaide in 1838, basically following the course of the Murray River after crossing it near Howlong. His journal (Hawdon 1952) contains many accounts of encounters with kangaroos (Eastern Grey Kangaroo); no doubt later encounters, as he travelled westwards, were with Western Grey Kangaroos and the Red Kangaroo, *Macropus rufus*. However, he did not distinguish between the species in his account. He collected two different types of small kangaroo. One was a 'small kangaroo of a fawn colour, with a most beautiful head, and about the size of an English hare' (probably Rufous Bettong, *Aepyprymnus rufescens*) and, the other had 'head and fur similar to those of a hare, with hairy hind feet, about the size of rabbit' (probably Eastern Hare-wallaby, *Lagorchestes leporides*). He recorded that the natives caught 'different species of kangaroo, from the large-sized one, weighing 100 pounds, to the small Kangaroo rat'. The latter was probably one of the species of *Bettongia*, either Burrowing Bettong, *B. lesueur* or Brush-tailed Bettong, *B. penicillata*. However, there are no acceptable records of *B. lesueur* being present in Victoria at

the time of contact (Menkhorst 1987). Hawdon had also seen 'a mouse of the kangaroo tribe' (Mitchell's Hopping-mouse, *Notomys mitchelli*), but did not record where that event occurred.

Major Sir Thomas Mitchell made the first scientific expedition into Victoria in 1836 (see Eeeleston 1992:32 for a map of his route through western Vietoria) and, although his journal (Mitchell 1839) does not contain records of many mammal species, it is notable for its original deseriptions of Pig-footed Bandicoot, *Chaeropus ecaudatus* [the only reeord from Victoria (Wakefield 1966; Menkhorst and Seebeck 1990]) and Mitehell's Hopping-mouse, and for first reports in Victoria of Platypus, *Ornithorhynchus anatinus*, and the rodents *Conilurus albipes* (Rabbit-eared Tree-rat), *Leporillus conditor* (Greater Stick-nest Rat) and *L. apicalis* (Lesser Stick-nest Rat) (Mahoncy 1982). Eccleston (1992) pinpoints the eapture location of *Conilurus albipes* to near modern-day St Arnaud, but casts some doubt as to whether either species of the stick-nest rats was actually colleeted in Vietoria. I have retained both species in Table 1 for now. Mitchell also recorded kangaroos (and most eertainly would have encountered Eastern and Western Grey Kangaroos and Red Kangaroo), possums (Common Brushtail Possum) and Dingo. His eompilation of a native voeabulary ineludes words for bandieoot but the species to which this may refer is unclear.

The growth of knowledge about native mammals aeeelerated, as settlers and hunters beeame familiar with the bush and its inhabitants.

Dr Edmund Hobson, who lived in Vietoria between 1839 and 1848 established an anatomieal museum and provided speeimens of Australian fauna to Sir Riehard Owen in London. In 1839 he recorded, on the Mornington Peninsula, Eastern Quoll, *Dasyurus viverrinus*; 'Peramelis or bandi-coot' (probably *Isoodon obesulus*, but perhaps *Perameles nasuta*; this latter species has only reeently (1989) been recorded for the Peninsula); Koala; Wombat; Common Brushtail Possum; Common Ringtail Possum, *Pseudocheirus peregrinus*; Feathertail Glider, *Acrobates pygmaeus* and Eastern Grey Kangaroo (Kenyon 1930). In that same year he travelled from Melbourne to the Murray River with Lady Franklin, and reeorded many native mammals, the most signi-ficant being the capture by a cat of a 'fine "rabbit rat"'; his deseription identifies it as *Conilurus albipes*. The streams (Goulburn, Broken, Ovens and Murray Rivers) and lagoons teemed with Platypus and Water Rat, *Hydromys chrysogaster*, and the forests supported Common Brushtail Possum, phalangers (probably Sugar Glider, sinee he describes other as 'flying squirrels ... their shrill sereams'—i.e. Yellow-bellied Glider, *Petaurus*

MONOTREMATA	MACROPODIDAE
Tachyglossus aculeatus	*Lagorchestes leporides*
Ornithorhynehus anatinus	*Maeropus fuliginosus*
	M. giganteus
DASYURIDAE	*M. robustus*
Antechinus swainsonii	*? M. rufogriseus*
Dasyurus maculatus	*M. rufus*
D. viverrinus	*Thylogale billardierii*
Phaseogale tapoatafa	*Wallabia bicolor*
Sminthopsis crassicaudata	
	PHASCOLARCTIDAE
PERAMELIDAE	*Phascolarctos cinereus*
Chaeropus eeaudatus	
Isoodon obesulus	VOMBATIDAE
Perameles nasuta	*Vombatus ursinus*
P. gunnii	
	CHIROPTERA
PHALANGERIDAE	*? Pteropus poliocephalus*
Trichosurus vulpecula	*? Pt. scapulatus*
ACROBATIDAE	RODENTIA
Acrobates pygmaeus	*Conilurus albipes*
	Hydromys chrysogaster
PETAURIDAE	*Leporillus apicalis*
Petaurus australis	*L. conditor*
P. brevieeps	*Notomys mitchelli*
Pseudocheirus peregrinus	*? Rattus fuscipes*
Petauroides volans	*? R. lutreolus*
POTOROIDAE	CANIDAE
Aepyprymnus rufescens	*Canis familiaris*
? Bettongia gaimardi	
? B. lesueur	
? B. penieillata	
? Potorous tridaetylus	
? P. longipes	

? indicates that I am not eonfident of the specific identity of mammals reported in contemporary accounts.

Table 1. Native mammals reported from Victoria before the establishment of the National Museum of Victoria in 1854.

australis or 'squirrels', probably Greater Glider, *Petauroides volans*), Dingoes, dasyuri (i.e. *D. viverrinus*) and kangaroo (Kenyon 1932; Parris 1950).

Daniel Bunee landed at Port Phillip in October 1839, and soon after explored the country towards Western Port. He was the first rccorded European to explore the Dandenong Ranges. He travelled with a group of Aboriginals and ate what was hunted by them—Common Brushtail Possum; 'Flying Squirrel' (probably *P. australis*, sinee he reported that lyrebirds mimieked 'the chuckle of the flying squirrel'); Koala; Wombàt; 'Wollabee'—probably Black Wallaby; kangaroo (*M. giganteus*) and Short-beaked Echidna, *Tachyglossus aculeatus* (Bunee 1859).

George Arden extolled the virtues of 'Australia Felix, the finest provinee of the Great Territory of New South Wales' to new immigrants in 1840, and, among the natural resourees he listed

	Forbes-Leith & Lucas	Lucas	Iredale & Troughton[1]	Mahoney	Brazenor	Wakefield	Warneke	Franken-berg	Menkhorst	Menkhorst	DCE
	1884	1890	1934	1935	1950	1963	1963	1971	1983	1987	1991
Order Monotremata											
Family Tachyglossidae											
Tachyglossus aculeatus	+	+	+	+	+	+	+	+	+	+	+
Family Ornithorhynchidae											
Ornithorhynchus anatinus	+	+	+	+	+	+	+	+	+	+	+
Order Marsupialia											
Family Dasyuridae											
Antechinomys laniger	+	+	+						*	*	*
Antechinus flavipes[2]	+	+	+	+	+	+	+	+	+	+	+
A. minimus[2]						+	+	+	+	+	+
A. stuartii[2]						+	+	+	+	+	+
A. swainsonii[2]	+	+	+	+	+	+	+	+	+	+	+
Dasyurus geoffroii	+	+	+	*	*				*	*	*
D. maculatus	+	+	+	+	+	+	+	+	+	+	+
D. viverrinus	+	+	+	+	+	+	+	+	*	*	*
Ningaui yvonneae									+	+	+
Phascogale calura	+	+	+		*				*	*	*
P. tapoatafa	+	+	+	+	+	+	+	+	+	+	+
Planigale gilesi										+	+
Sminthopsis crassicaudata				+	+	+	+	+	+	+	+
S. leucopus	+	+	+		+	+	+	+	+	+	+
S. murina	+	+	+		+	+		+	+	+	+
Family Peramelidae											
Chaeropus ecaudatus	+	+	+						*	*	*
Isoodon obesulus	+	+	+	+	+	+	+	+	+	+	+
Isoodon sp. (cf. *auratus*)										*	
Perameles bougainville	+	+	+						*	*	*
P. gunnii	+	+		+	+	+	+	+	+	+	+
P. nasuta	+	+	+	+	+	+	+	+	+	+	+
Family Phalangeridae											
Trichosurus caninus	+	+		+	+	+	+	+	+	+	+
T. vulpecula	+	+	+	+	+	+	+	+	+	+	+
Family Burramyidae											
Acrobates pygmaeus	+	+	+	+	+	+	+	+	+	+	+
Burramys parvus								+	+	+	+
Cercartetus concinnus						+	+	+	+	+	+
C. lepidus									+	+	+
C. nanus	+	+	+	+	+	+	+	+	+	+	+
Family Petauridae											
Gymnobelideus leadbeateri		+	+	*	*	+	+	+	+	+	+
Petaurus australis	+	+	+	+	+	+	+	+	+	+	+
P. breviceps	+	+	+	+	+	+	+	+	+	+	+
P. norfolcensis	+	+	+	+	+	+	+	+	+	+	+
Family Pseudocheridae											
Pseudocheirus peregrinus	+	+	+	+	+	+	+	+	+	+	+
Petauroides volans	+	+	+	+	+	+	+	+	+	+	+
Family Potoroidae											
Aepyrymus rufescens	+				*	*			*	*	*
Bettongia gaimardi	+	+			*	*			*	*	*
B. penicillata	+		+			*			*	*	*
Potorous longipes									+	+	+
P. tridactylus				+	+	+	+	+	+	+	+

Table 2.   Mammals recorded for Victoria by various authors between 1884 and 1991.   * Recorded as extinct.

	Forbes-Leith & Lucas 1884	Lucas 1890	Iredale & Troughton[1] 1934	Mahoney 1935	Brazenor 1950	Wakefield 1963	Warneke 1963	Franken-berg 1971	Menkhorst 1983	Menkhorst 1987	DCE 1991
Order Marsupialia (continued)											
Family Macropodidae											
Lagorchestes leporides	+	+		*	*				*	*	*
Macropus fuliginosus	+	+	+		+			+	+	+	+
M. giganteus	+	+	+	+	+	+	+	+	+	+	+
M. greyi										*	*
M. robustus						+	+	+	+	+	+
M. rufogriseus	+	+	+	+	+	+	+	+	+	+	+
M. rufus	+	+	+		+	+	+	+	+	+	+
Onychogalea fraenata	+	+	+						*	*	*
Petrogale penicillata	+	+			+	+	+	+	+	+	+
Thylogale billardierii		+	+	*	*	*			*	*	*
Wallabia bicolor	+	+	+	+	+	+	+	+	+	+	+
Family Phascolarctidae											
Phascolarctos cinereus	+	+	+	+	+	+	+	+	+	+	+
Family Vombatidae											
Vombatus ursinus	+	+	+	+	+	+	+	+	+	+	+
Order Chiroptera											
Family Pteropodidae											
Pteropus poliocephalus	+	+	+	+	+	+	+	+	+	+	+
P. scapulatus			+					+	+	+	+
Family Rhinolophidae											
Rhinolophus megaphyllus						+	+	+	+	+	+
Family Emballonuridae											
Saccolaimus flaviventris				+	+	+	+	+	+	+	+
Family Molossidae											
Mormopterus planiceps						+	+	+	+	+	+
Mormopterus sp. 1											+
Mormopterus sp. 2											+
Tadarida australis	+	+			+	+	+	+	+	+	+
Family Vespertilionidae											
Chalinolobus gouldii			+	+	+	+	+	+	+	+	+
C. morio			+		+	+	+	+	+	+	+
E. 'pumilus'[3]			+	+	+	+	+	+			
Eptesicus baverstocki[3]										+	+
E. darlingtoni[3]									+	+	+
E. regulus[3]									+	+	+
E. vulturnus[3]									+	+	+
Falsistrellus tasmaniensis								+	+	+	+
Miniopterus schreibersii						+	+	+	+	+	+
Myotis adversus						+	+	+	+	+	+
Nyctophilus geoffroyi			+	+	+	+	+	+	+	+	+
N. gouldi									+	+	+
N. timoriensis[4]						+		+	+	+	+
Scotorepens balstoni									+	+	+
S. orion										+	+
Order Rodentia											
Family Muridae											
Conilurus albipes	+	+			*				*	*	*
Hydromys chrysogaster	+	+		+	+	+	+	+	+	+	+
Leporillus apicalis				*					*	*	*

Table 2 (continued).

	Forbes-Leith & Lucas 1884	Lucas 1890	Iredale & Troughton[1] 1934	Mahoney 1935	Brazenor 1950	Wakefield 1963	Warneke 1963	Franken-berg 1971	Menkhorst 1983	Menkhorst 1987	DCE 1991
Order Rodentia *(continued)*											
Family Muridae *(continued)*											
L. conditor	+	+			*			*	*	*	*
Mastacomys fuscus			+	+	+	+	+	+	+	+	+
Notomys mitchelli	+	+	+	+	+	+	+	+	+	+	+
Pseudomys apodemoides							+	+	+	+	+
P. australis					*	*			*	*	*
P. desertor										*	*
P. fumeus				+	+	+	+	+	+	+	+
P. hermannsburgensis[5]	+	+			*				*	*	*
P. novaehollandiae[5]							+	+	+	+	+
P. shortridgei									+	+	+
P. sp. nov.						+				*	*
Rattus fuscipes	+	+	+	+	+	+	+	+	+	+	+
R. lutreolus			+	+	+	+	+	+	+	+	+
Order Carnivora											
Family Canidae											
Canis familiaris	+	+	+	+	+	+		+	+	+	+
Halmaturus brachyurus[6]	+										
H. thetidis[6]	+										
Bettongia grayi[7]	+					*					
Macrotis lagotis[8]	+		+	*	*						
Onychogalea lunata[9]		+									
Petrogale xanthopus[10]			+								
Pseudomys gouldii[11]					*						
Pseudomys oralis[11]						*					
Scoteinus sp.[12]							+				

Table 2 (continued).

[1] Iredale & Troughton (1934) made no assessments of status, so that a number of species which were known to be extinct in Victoria are included together with extant species.

[2] Until the early 1960s when Wakefield & Warneke (1963, 1967) resolved the taxonomic confusion, specimens of *Antechinus* were assigned to either *A. flavipes* or *A. swainsonii*. Wakefield & Warneke (1963) demonstrated that *A. minimus did* occur in Victoria and in 1967 published a rationalisation of *A. 'flavipes'*, showing that *A. stuartii* and *A. flavipes* both occurred in the State.

[3] '*Eptesicus pumilus*' includes four species, now assigned to the genus *Vespadelus*: *V. baverstocki*, *V. darlingtoni*, *V. regulus* and *V. vulturnus* (Kitchener et al. 1987; Volleth & Tidemann 1989, 1991).

[4] *Nyctophilus 'timoriensis'* as here recognised was shown to be *N. gouldi* by Hall & Richards (1979), but true *N. timoriensis* is now recorded for Victoria (Robertson et al. 1989).

[5] *Mus novaehollandiae* was applied to specimens collected by Blandowski, which were identified as *Pseudomys hermannsburgensis* by Wakefield (1966). Brazenor (1950), who had noted the similarity between the species, considered *P. novaehollandiae* to be extinct although Troughton had 'correctly' identified the Blandowski animals as *P. hermannsburgensis* a decade earlier. Wakefield (1960) discovered *P. novaehollandiae* as a sub-fossil in caves in eastern Victoria and hence included it in his 1963 list; it was discovered as a living species in the State in 1970 (Seebeck & Beste 1970). Kemper (pers. comm.) examined the Blandowski material and concluded that it was *P. bolami*. Kitchener et al. (1984) incorporated *P. 'hermannsburgensis'* from Victoria in *P. bolami*.

[6] *Halmaturus brachyurus* = *Setonyx brachyurus*, which is confined to Western Australia. *H. thetidis* = *Thylogale thetis*, of northern NSW and Queensland. One of these names is in error for *Thylogale billardierii* which was well-known for the State, although it is now extinct on the mainland.

[7] There is no evidence confirming that *B. lesueur* (= *B. grayi*) was extant in Victoria at the time of contact (Menkhorst 1987b; Menkhorst & Seebeck 1990) but it is present as a fossil in south-western Victoria (Wakefield 1972).

[8] Menkhorst & Seebeck (1990) have demonstrated that there is no evidence to include *M. lagotis* in the modern Victorian fauna.

[9] This was included by Wakefield on the basis of sub-fossil material only; there are no data to suggest it was extant in Victoria at the time of contact.

[10] Probably a misunderstanding. It should be *P. penicillata*.

[11] Both included on the basis of sub-fossil material. There is no evidence of either species being extant at time of contact.

[12] *Scoteinus* now = *Scotorepens*; at the time (1963) it was tentatively assigned to *S. greyi*.

Mitchell's Hopping-mouse, 'the different species of kangaroo and opossum tribes, the wombat, a kind of badger which burrows deep in the ground; a species of sloth, unnamed, which evinces a most extraordinary predilection for fur, and will hug a cat to death (I presume the 'sloth' to be the koala – but cannot explain the reputed cat-killing behaviour); the devil and opossum hyaena, formerly supposed to be peculiar to Van Dieman's Land; and the native dog.' The Platypus was frequently seen, and 'a species of wild cat prowls in the neighborhood of civilization, and is most destructive to poultry' (Arden 1840). (Both *D. viverrinus* and the Tiger Quoll, *D. maculatus*, have frequently been recorded as preying on poultry.) The Tasmanian Devil (*Sarcophilus harrisi*) and Thylacine, *Thylacinus cynocephalus* (for which 'opossum hyaena' was an early vernacular) did *not* occur in Victoria, despite Mr Arden's enthusiasm.

Joseph Lingard (1846) was a professional hunter in the Monaro district and the adjacent area of far east Gippsland during 1842–43. His list of species is extensive – 'Wild Ferret' (*D. viverrinus*); bandicoot (at that locality Long-nosed Bandicoot, *Perameles nasuta*); Wombat; Koala; 'Flying Mouse' (*A. pygmaeus*); Common Brushtail Possum; Common Ringtail Possum; kangaroo rat (probably Long-footed Potoroo, *Potorous longipes*); kangaroo (*M. giganteus*); Common Wallaroo (*Macropus robustus*); Brush-tailed Rock-wallaby (*Petrogale penicillata*); Dingo; and 'Flying Fox' (*Pteropus*, probably Grey-headed Flying-fox, *P. poliocephalus*, but perhaps Little Red Flying-fox, *P. scapulatus*, as well); and 'Squirrel'. These were taken for skins, so it is most likely they were *Petauroides volans* and/or *Petaurus australis* (he refers to the squirrels 'screaming' at night, indicating *P. australis* which has a wide repertoire of vocalisation; *P. volans* is almost silent).

William Lockhart Morton (Randell 1978) travelled widely in Victoria from 1842 onwards. In that year he recorded kangaroos (*M. giganteus*) and Dingo near Camperdown; in 1843 'native cat' (*D. viverrinus*) at Drysdale; and Short-beaked Echidna at Mt Alexander in 1845. In 1847 he was at Watchem, in the southern Mallee, and encountered kangaroos (probably Western Grey Kangaroo) and Dingo.

William Brodribb (1883) recounted that an aboriginal named Charley Tara had caught Koalas to feed Count Paul Strzelecki during his explorations in west Gippsland in 1840. An account of Strzelecki's journey, published in the Port Phillip Herald in June 1840, reported that Charley also caught Common Wombats and kangaroos to feed the party (Heney 1961). Brodribb himself explored in Gippsland in 1842, and reported the presence of large numbers of Rabbits on Rabbit Island off Wilson's Promontory, as well as many kangaroos (Eastern Grey Kangaroo) in the area now known as Port Albert. Note that this was three years before Thomas Austin's successful mainland introduction of Rabbits; they had been introduced to Rabbit Island in 1836 (Stokes 1846). Brodribb further noted 'opossum' (*T. vulpecula*) and 'kangaroos' near the Latrobe River. During his return to Western Port he, like Strzelecki, had to be fed by his aboriginal assistant, the same Charley Tara, who again displayed his skills at catching Koalas ('almost every day') as well as possums and bandicoots (in that area probably Long-nosed Bandicoot).

George Henry Haydon, writing to educate potential colonists (he was in Victoria during 1840–45, and was in the first party to traverse west Gippsland, accompanying G. A. Robinson in 1844) listed Platypus; bandicoot; Common Wombat; Koala; 'brushtail' possum (both Common Brushtail Possum and Mountain Brushtail Possum, *Trichosurus caninus*, may have been encountered); Common Ringtail Possum; 'Flying Squirrel' – he described both *P. volans* and *P. breviceps*; 'Pademelon' (*T. billardierii*); kangaroo; wallaby and kangaroo rat (his description suggests Tasmanian Bettong, *Bettongia gaimardi*, rather than Long-nosed Potoroo, *Potorous tridactylus*) as well as Dingo and 'rats' (Haydon 1846).

Another such colonial educator was Dr James Clutterbuck, who, on returning to London in 1849, quickly published his advice (Clutterbuck 1850). Although he claimed no specialist knowledge of such matters, he listed Platypus, 'Wild Cat' (probably *D. viverrinus* but may also have included *D. maculatus*) – whose skins made 'handsome rugs'; bandicoot; Koala; 'Flying Squirrel'; 'possum' ('of the rat species'!) – Common Brushtail Possum (also good for rugs; a six-foot-square rug cost 30 shillings); 'kangaroo rat' (probably *Potorous* sp.); Eastern Grey Kangaroo; Brush-tailed Rock-wallaby – and here his lack of knowledge emerged again, as he listed 'Rock Wallaby, or Badger, of the family of kangaroos'; Common Wombat; Dingo; and also noted the presence of Brown Rat and mouse. It is probable that this is the first published report of these introduced rodents (Brown Rat, *Rattus norvegicus* and House Mouse, *Mus musculus*) in Melbourne, rather than a confusion with native species.

The Sunbury district was first settled in 1836, and the family of Isaac Batey moved there 10 years later. In 1907 Batey set down his recollections of the 'Animal-life of the Sunbury district sixty years ago' (Batey 1907) and listed a wide range of species with which he had been familiar during the 1840s.

Bandicoot, brown: Southern Brown Bandicoot, *Isoodon obesulus*

Bandicoot, banded: Eastern Barred Bandicoot, *Perameles gunnii*

Bat, common: No specific identification possible

Bat, vampire or flying fox: Grey-headed Fruit-bat, *Pteropus poliocephalus* [Little Red Fruit-bat, *P. scapulatus* is an occasional vagrant to western Victoria]

Bear, or sloth; Bear, young one on mother's back: Koala, *Phascolarctos cinereus*

Bull; Bullock, worker; Cattle; Cow, milch: Cattle, *Bos taurus*

Cat, domestic: Cat, *Felis catus*

Dasyure, black and spotted native cat; Dasyure, brown and spotted native cat: Eastern Quoll, *Dasyurus viverrinus*

Dog, domestic; Dog, wild; Dog, wild female; Dog, Barrukills dog: Dog, *Canis familiaris* and Dingo, *C. f. dingo*

Foal; Horse: Horse, *Equus caballus*

Jerboa, or bilboa: Scarlett (1969) identified this as the Greater Bilby, *Macrotis lagotis*, but Menkorst & Seebeck (1990) did not accept that identification. They suggested that the term may have referred to Burrowing Bettong, *Bettongia lesueur*, but considered the identification equivocal, as there is no evidence that that species was extant at the time of European settlement in Victoria.

Kangaroo, general name; Kangaroo, old male; Kangaroo, young male; Kangaroo, flying doe; Kangaroo, joey: Both Eastern (*Macropus giganteus*) and Western (*M. fuliginosus*) Grey Kangaroo, are probably included, the latter especially in the language used by northern tribes.

Kangaroo, red: Red Kangaroo, *Macropus rufus* [This species generally does not occur south of the Mallee; perhaps Dawson was told about it, or was confused with the following species]

Kangaroo, brush: Red-necked Wallaby, *Macropus rufogriseus*

Kangaroo, wallaby: Black Wallaby, *Wallabia bicolor*

Kangaroo rat: Long-nosed Potoroo, *Potorous tridactylus*

Kangaroo mouse: ?Mitchell's Hopping Mouse, *Notomys mitchellii* [As with the Red Kangaroo, this species does not occur south of the Mallee. Perhaps the name referred to one of the other native rodents, or to one of the small dasyurid marsupials]

Opossum, common; Opossum, old male; Opossum, old female; Opossum, young, in pouch: Common Brushtail Possum, *Trichosurus vulpecula*

Opossum, ringtail: Common Ringtail Possum, *Pseudocheirus peregrinus*

Platypus: Platypus, *Ornithorhynchus anatinus*

Porcupine, ant-eater: Short-beaked Echidna, *Tachyglossus aculeatus*

Rat, British rat: Either Black Rat, *Rattus rattus* or Brown Rat, *R. norvegicus*

Rat, rabbit-rat: Rabbit-eared Tree-rat, *Conilurus albipes*

Rat, water-rat: Water Rat, *Hydromys chrysogaster*

Sheep: Sheep, *Ovis aries*

Squirrel, large flying: Yellow-bellied Glider, *Petaurus australis*

Squirrel, small flying: Sugar Glider, *Petaurus breviceps*

Squirrel, feather-tailed: Feathertail Glider, *Acrobates pygmaeus*

Swine: Pig, *Sus scrofa*

Wombat: Common Wombat, *Vombatus ursinus*

Table 3. Mammals included in James Dawson's language list which was compiled from western Victorian dialects, representing three language groups (from Dawson 1881). The list presents Dawson's English name; the modern vernacular; and the scientific name.

He reported the following: Platypus; Swainson's Antechinus, *Antechinus swainsonii*; Eastern Quoll; Tiger Quoll; Brush-tailed Phaseogale, *Phascogale tapoatafa*; Fat-tailed Dunnart, *Sminthopsis crassicaudata*; 'short-tailed Bandicoot, *Perameles* sp.' (Eastern Barred Bandicoot, *Perameles gunnii*); Koala; Common Wombat; Common Brushtail Possum; Common Ringtail Possum; Sugar Glider; Greater Glider; Water Rat and Dingo.

Even incidental records added to the identifiable species. Stokes (1846) landed on Phillip Island in January 1839, and disturbed 'a kangaroo, very dark colored, indeed almost black'. This was certainly the Black Wallaby.

James Dawson was one of the outstanding pioneers of the Western District. He settled near Port Fairy in 1844, and lived there until 1866, when he was forced to sell up. He returned to live near Camperdown until his death in 1900. During his many years in western Victoria, he studied the language and customs of the Aborigines, and in his account of their society (Dawson 1881) he published lists of three language group names of mammals, in addition to extensive vocabularies for many other aspects of Aboriginal life. The list of mammals includes native and introduced species' names, and is often very specific—separate words for male and female, old and young, were recorded for some species. The list of forms with separate names is given in Table 3.

George Augustus Robinson, Protector of Aborigines, toured parts of eastern and western Victoria from 1840 to 1849, and recorded extensive natural history observations (Mackaness 1941; Presland 1977a, 1977b, 1980; Clark 1988). He added mostly only local records of known species but did record evidence of other species for the first time, e.g. Plains Mouse, *Pseudomys australis* (Seebeck 1984).

Mansergh and Hercus (1981) listed and discussed some Gippsland aboriginal names for mammals. The sources upon which they based their work included two from the 1840s and 1850s, but most were from somewhat later in the century. Mountain Brushtail Possum, Common Brushtail Possum, either Yellow-bellied Glider or Greater Glider, potoroo, Eastern Grey Kangaroo, Red-bellied Pademelon, Brush-tailed Rock-wallaby, Dingo, Horse and Cattle were recorded in one or other language list before the mid-1850s. Many other species were recorded in later listing, including one of the few records of the White-footed Rabbit-rat.

Table 1 lists the species of non-marine mammal reported in Victoria prior to 1854.

RECORDS SINCE 1854

By the time William Blandowski was appointed

Zoologist to the new Museum of Natural History, on 1 April 1854 (Pescott 1954), the list of species known for the State was substantial (Table 1). Eight months later, Blandowski (1855a) was able to provide what was, in effect, the first formal list of species for the State, although some of the forms he described were not 'species' and there were, in addition, some species of which he was aware but was unable to make comment upon. He listed 29 forms—probably representing 26 or 27 species.

Pescott (1954) suggested that Blandowski may have begun to make a formal checklist of species, but, if he did so, the list has been lost. T. Darragh (Museum of Victoria, pers. comm. 1987) is not convinced that such a checklist was prepared.

During the 1850s Blandowski, and Gerard Krefft carried out surveys that added materially to the State's known fauna—in fact, their efforts provided the only records of some species for Victoria, particularly those of the semi-arid northwest of the State (Blandowski 1855a, 1855b; Krefft 1866; Wakefield 1966; Bennett et al. 1989).

In addition to such scientific enterprise, others were observing and recording their knowledge. Perhaps the most significant, in retrospect, was Horace Wheelwright, who was a professional hunter for the Melbourne market during the mid-1850s. Although his published account (Wheelwright 1861) lists only 26 species, mostly marsupials, it provides a specific local fauna for the vicinity of Melbourne. It also records many valuable observations on the habits of the animals encountered.

James Bonwick, Inspector of Denominational Schools, Victoria, toured western Victoria for three months in 1857. His account (Bonwick 1858) includes many reports of encounters with mammals, including Common Wombat, Water-rat, Platypus, Koala, possums (probably Common Brushtail Possum, as the skins were used by Aborigines), Dingo, 'opossum mice' (probably Eastern Pigmy-possum, *Cercartetus nanus*), 'perro' (probably Long-nosed Potoroo), kangaroos (probably Eastern Grey Kangaroo), bats (from caves in the Stoney Rises; the Common Bent-wing Bat, *Miniopteris schreibersii* is known from Mt Porndon Cave); and 'wild cats', which may have been Tiger Quoll or Eastern Quoll or perhaps feral cats. Bonwick refers to the 'wild cats' living in caves, and their 'most undescribable . . .; repulsive growls' when disturbed. Both quolls and cats are capable of distinctive vocalisation.

Bonwick also commented upon the then recent discovery and description of *Thylacoleo carnifex*, the 'Marsupial Lion' and other extinct megafauna from near Colac, and other fossil mammals from near Portland and Mt Gambier.

W. L. Morton, who had earlier travelled in western Victoria (see Randall 1978) made an extensive tour of the Wimmera and southern Mallee in 1861. He published an account of that trip anonymously in 1861 and 1862 (An Old Bushman 1861/1862); that account was edited and reprinted by the National Parks Authority over a century later (Morton 1966). He recorded several instances of 'wallaby', 'paddymelon' and 'kangaroo rat' being hunted by his dogs, and described the nests of the latter two animals. The wallaby was likely to have been the Bridled Nail-tail Wallaby, *Onychogalea fraenata* (recorded by Krefft [1866] as 'common'); another possibility is Red-necked Wallaby, but that species generally occurs further south; the 'paddymelon' and 'kangaroo rats' were probably Eastern Hare-wallaby and Brushtailed Bettong. Morton also recorded opossum (probably Common Brushtail Possum, since he took them for skins) and Common Ringtail Possum.

FORMAL LISTS OF SPECIES

The first published catalogue of Victorian native mammals appeared in 1884 (Forbes-Leigh & Lucas 1884). This contained the names of 52 species of non-marine mammals—2 monotremes, 41 marsupials, 6 rodents, 2 bats and the Dingo.

Six years later Lucas (1890) prepared as account of the fauna of Victoria for the Australasian Association for the Advancement of Science. His list was slightly shorter than the earlier one (50), and included several species not listed in 1884; it did not include a number that had been listed. He recognised that some species were already becoming scarce, and, by the omission of certain species, must also have recognised that some were no longer present in Victoria.

Ogilby's (1892) Catalogue stated or implied the occurrence in Victoria of 54 mammal species. Eight of these were bats, but only one (Chocolate Wattled Bat, *Chalinolobus morio*) was specifically recorded for Victoria. The other seven species were reported for 'Eastern Australia', or 'Australia', so that comparisons with other lists can not be made with confidence.

By the mid-1930s (Iredale & Troughton 1934; Mahoney 1935) the total was little altered—56 species including 39 marsupials, 6 rodents and 8 bats. However, there had been changes in recognition and identification of the species present—some because they had become extinct, others by acceptance that the taxon did not, in fact, occur in Victoria. The greatest change was in the number of bat species recorded. It should be noted, also, that '*Eptesicus pumilus*' is now recognised to consist of four species in the genus *Vespadelus*—

V. baverstocki, V. darlingtoni, V. regulus and *V. vulturnus*—but these taxonomic distinctions have only recently been recognised (McKean et al. 1978; Kitchener et al. 1987; Volleth & Tidemann 1989, 1991).

In 1924 Charles Brazenor was appointed to the National Museum of Victoria as a preparator; later he became Mammalogist. During his years at the Museum knowledge of the Victorian mammal fauna, particularly the rodents, increased markedly. In 1950 he published 'The Mammals of Victoria', containing a list of 59 species of non-marine mammals (Brazenor 1950).

Some years later Warneke (1963) published a mammal checklist for the State. The list included only extant species and *D. viverrinus*, which had last been recorded in 1955 and might still have been extant. Of the 54 species he included, 32 were marsupials, 7 were rodents and 12 were bats. In the same year Wakefield (1963) contributed 'Mammals of Victoria' to the Victorian Year Book, and included in the article the names of 54 extant and 9 extinct species. But he included several species not listed by Warneke—who in turn, had listed two species not listed by Wakefield (see Table 2).

Twenty years later Menkhorst (1983) compiled a Working List which, in listing 69 extant species reflected the upsurge in survey effort and taxonomic rationalisation that had taken place. That increase had come about largely because of the introduction of new techniques of survey, and by new techniques of biological assessment. For example, two dasyurid genera, *Ningaui* (in 1977) and *Planigale* (in 1986) were recorded by the use of pitfall traps in semi-arid zones (Fleming & Cockburn 1979; Lumsden et al. 1988), as was the Little Pygmy-possum *Cercartetus lepidus* (Dixon 1978), and many bat taxa have been found by the use of harp traps (Emison et al. 1984). Differentiation of species in several taxa of bats has been due primarily to modern biochemical and cytological techniques coupled with traditional methods.

A revised list (Menkhorst 1987b) reported the presence of 70 extant non-marine species. This list included a number of taxonomic changes, the addition of four species and the deletion of two others.

The 1991 list (DCE 1991) published in the Department's Wildlife Manual included an additional two species of bats but inadvertently omitted one species of bandicoot formerly present. Taxonomic reappraisal has shown that the rodent species *Pseudomys 'hermannsburgensis'* recorded for north-western Victoria is *P. bolami* (Kitchener

et al. 1984; C. M. Kemper, pers. comm.). This list also considered the Dingo as an introduced species.

Table 2 provides a summary of the species recognised by the authors quoted above.

This resumé serves to illustrate the spasmodic, at times rapid, accumulation of knowledge of even such a closely-studied group as the mammals. Many taxa were well known soon after the beginnings of European settlement—Wheelwright (1861) found it 'a matter of surprise to me that so much is already known of the general Fauna of this land'—but the smaller species were slow to be recognised. Nevertheless, all species of terrestrial mammals larger than 'rat-sized' (with one exception, *Potorous longipes* [Seebeck & Johnston 1980]) had been recorded for the State by the turn of the century, a tribute to the skills of the local natural historians.

What of the future? There are a few bat species which might be found to range into Victoria, and there may be other small terrestrial species present in the semi-arid north-west of the State, but most changes to the list of species are likely to result from taxonomic revision rather than by new discoveries.

ACKNOWLEDGEMENTS

REFERENCES

An Old Bushman (W. L. Morton), 1861–62. Notes of a tour in the Wimmera District. *The Yeoman, and Australian Acclimatizer*, Vol. 1.

(ARDEN, G.), 1840. *Latest Information With Regard to Australia Felix, the Finest Province of the Great Territory of New South Wales; including the History, Geography, Natural Resources, Government, Commerce and Finances of Port Phillip; sketches of the Aboriginal Population, and Advice to Immigrants; by the Editor of the Port Phillip Gazette, Melbourne.* Arden & Strode, Printers, Melbourne. [1977 facsimile edition by Queensberry Hill Press, Carlton.]

AUSTIN, K. A., 1974. *Matthew Flinders on the Victorian Coast.* Cypress Books, Melbourne.

BARKER, R. D. & CAUGHLEY, G., 1992. Distribution and abundance of kangaroos (Marsupialia: Macropodidae) at the time of European contact: Victoria. *Australian Mammalogy* 15: 81–88.

BASSETT, M., 1954. *The Hentys. An Australian Colonial Tapestry.* Oxford University Press, London.

BATEY, I., 1907. The animal life of the Sunbury district sixty years ago. *Victorian Naturalist* 24: 69–74.

BENNETT, A. F., LUMSDEN, L. F. & MENKHORST, P. W., 1989. Mammals of the mallee region of south-eastern Australia. In *Mediterranean Landscapes in Australia: Mallee Ecosystems and their Management.* CSIRO, Melbourne. Noble, J. C. & Bradstock, R. A. (eds), 191–220.

BLAND, W., 1831. *Journey of Discovery to Port Phillip, New South Wales: by Messrs. W. H. Hovell, and Hamilton Hume: in 1824 and 1825.* A. Hill, Sydney. [1965 facsimile edition by Libraries Board of South Australia.]

BLANDOWSKI, W., 1855a. Personal observations made in an excursion towards central parts of Victoria, including Mount Macedon, McIvor, and Black Ranges. *Transactions of the Philosophical Society of Victoria* 1: 50–74.

BLANDOWSKI, W., 1855b. Report, No. III, to the Surveyor-General, of an excursion from King's Station to Bass River, Phillip and French Islands. *Transactions of the Philosophical Institute of Victoria* 1: 50–67.

BONWICK, J., 1858. *Western Victoria. Its Geography, Geology, and Social Conditions.* Thomas Brown, Geelong. [New Edition, edited by C. E. Sayers, 1970. Heinemann, Melbourne.]

BRAZENOR, C. W., 1950. *The Mammals of Victoria* and The Dental Characteristics of Monotremes and Australian Marsupials. Handbook No. 1. National Museum of Victoria. Melbourne.

BRODRIBB, W. A., 1883. *Recollections of an Australian Squatter.* John Woods & Co., Sydney. [2nd Edition published by Queensberry Hill Press, Melbourne, 1976.]

BUNCE, D., 1859. *Travels with Dr. Leichhardt in Australia.* W. Fairfax & Co., Melbourne.

CLARK, I. D., 1988. The Port Phillip Journals of George Augustus Robinson: 8 March–7 April 1842 and 18 March–29 April 1843. Monash University, Melbourne, Victoria 3168.

CLUTTERBUCK, J. B., 1850. *Port Phillip in 1849.* John W. Parker, London.

DAWSON, J., 1881. *Australian Aborigines.* The Languages and Customs of Several Tribes of Aborigines in the Western District of Victoria, Australia. George Robertson, Melbourne. [1981 facsimile edition published by Australian Institute of Aboriginal Studies, Canberra.]

DCE (DEPARTMENT OF CONSERVATION AND ENVIRONMENT), 1991. Working list of Victorian Wildlife. Guideline No. 16, Wildlife Manual. Wildlife Branch, Flora and Fauna Division, Melbourne.

DIXON, J. M., 1978. Little Pigmy Possum in Victoria. *Victorian Naturalist* 95: 4–7.

ECCLESTON, G. C., 1992. Major Mitchell's 1836 'Australia Felix' Expedition: A Re-evaluation. *Monash Publications in Geography* No. 40. Monash University, Australia.

EMISON, W. B., MENKHORST, P. W., NORMAN, F. I., ROBERTSON, P., CORRICK, A. H. & ALDERSON, J. A., 1984. Wildlife surveys conducted by the Fisheries and Wildlife Division in Victoria, 1972–1983. In *Survey Methods for Nature Conservation, Vol. 2.* CSIRO and Division of Water and Land Resources, Canberra. Myers, K., Margules, C. R. & Musto, I. (eds), 166–194.

FERGUSON, J. A., 1941–1969. *The Bibliography of Australia.* Angus & Robertson, Sydney. [1975 facsimile edition, National Library of Australia, Canberra.]

FLEMING, M. R. & COCKBURN, A., 1979. *Ningaui*: a new genus of dasyurid for Victoria. *Victorian Naturalist* 96: 142–145.

FLINDERS, M., 1814. *A Voyage to Terra Australis; etc.* G. and W. Nicol, London. [1966 facsimile edition by Libraries Board of South Australia.]

FORBES-LEITH, T. A. & LUCAS, A. H., 1884. Catalogue of the fauna of Victoria. Vertebrata: Mammalia. *Victorian Naturalist* 1: 4–6.

FRANKENBERG, J., 1971. *Nature Conservation in Victoria. A Survey.* Victorian National Parks Association, Melbourne.

GRANT, J., 1803. *The narrative of a Voyage of Discovery, performed in His Majesty's Vessel the Lady Nelson, of Sixty Tons Burthen, with sliding Keels, in the years 1800, 1801, and 1802, to New South Wales.* T. Egerton, London. [1973 facsimile edition by Libraries Board of South Australia.]

HALL, L. S. & RICHARDS, G. C., 1979. *Bats of Eastern Australia.* Queensland Museum, Brisbane.

HAWDON, J., 1952. *The Journal of a Journey from New South Wales to Adelaide (The Capital of South Australia). Performed in 1838.* Georgian House, Melbourne.

HAYDON, G. A., 1846. *Five Years Experience in Australia Felix, comprising a short account of its early settlement and its present position, with many particulars interesting to intending emigrants.* Hamilton, Adams & Co., London.

HENEY, H. M. E., 1961. *In a Dark Glass.* The Story of Paul Edmund Strzelecki. Angus & Robinson, Sydney.

HIBBINS, G. M., 1984. *A History of the City of Springvale.* Constellation of Communities. City of Springvale and Lothian, Melbourne.

IREDALE, T. & TROUGHTON, E. LE, G., 1934. A Checklist of the Mammals Recorded from Australia. *Memoirs of the Australian Museum* 6: xi + 1–22.

KENYON, A. S., 1930. Our first Victorian naturalist: Dr. Edmund Charles Hobson. *Victorian Naturalist* 47: 94–98.

KENYON, A. S., 1932. From Port Phillip to Sydney in 1839. *Victorian Naturalist* 48: 213–221.

KITCHENER, D. J., ADAMS, M. & BAVERSTOCK, P., 1984. Redescription of *Pseudomys bolami* Troughton, 1932 (Rodentia: Muridae). *Australian Mammalogy* 7: 149–159.

KITCHENER, D. J., JONES, B. & CAPUTI, N., 1987. Revision of Australian *Eptesicus* (Microchiroptera: Vespertilionidae). *Records of the Western Australian Museum* 13: 427–500.

KREFFT, G., 1866. On the vertebrated animals of the lower Murray and Darling, their habits, economy, and geographical distribution. *Transactions of the Philosophical Society of New South Wales 1862* 65: 1–38.

LEARMONTH, N. F., 1934. *The Portland Bay Settlement, being the History of Portland, Victoria from 1800 to 1851.* McCarron, Bird & Co., Melbourne.

LEE, 1., 1915. *The Logbooks of the 'Lady Nelson' with the Journal of Her First Commander, Lieutenant James Grant, R.N.* Grafton & Co., London.

LINGARD, J., 1846. *A Narrative of the Journey to and from New South Wales, including a seven years residence in that Country.* J. Taylor, Chapel-en-le-Frith, Derbyshire.

LUCAS, A. H. S., 1890. Zoology: Vertebrata. In *Handbook of Melbourne.* Spectator Publishing Co., Melbourne. Spencer, W. B. (ed.), 56–73.

LUMSDEN, L. F., BENNETT, A. F. & ROBERTSON, P., 1988. First record of the Paucident Planigale, *Planigale gilesi* (Marsupialia: Dasyuridae), for Victoria. *Victorian Naturalist* 105: 81–87.

MACKANESS, G., 1941. *George Augustus Robinson's Journey into S.E. Australia, 1844, with George Henry Haydon's Narrative of Part of the Same Journey.* The Author, Sydney.

MCKEAN, J. L., RICHARDS, G. C. & PRICE, W. J., 1978. A taxonomic appraisal of *Eptesicus* (Chiroptera: Mammalia) in Australia. *Australian Journal of Zoology* 26: 529–537.

MAHONEY, D. J. (ed.), 1935. The Zoology of Victoria. In *Handbook for Victoria*, A.N.Z.A.A.S., Melbourne. Leeper, G. W. (ed.), 60–77.

MAHONEY, J. A., 1982. Identities of the rodents (Muridae) listed in T. L. Mitchell's 'Three Expeditions into the Interior of Eastern Australia, with Description of the Recently Explored Region of Australia Felix, and of the Present Colony of New South Wales' (1st edn, 1838; 2nd edn, 1839). *Australian Mammalogy* 5: 15–36.

MANSERGH, 1. & HERCUS, L. A., 1981. An Aboriginal vocabulary of the fauna of Gippsland. *Memoirs of the National Museum of Victoria* 42: 107–122.

MENKHORST, P. W., 1983. Working list of Victorian mammals. *Arthur Rylah Institute Technical Report Series* No. 7 (Fisheries and Wildlife Service, Victoria).

MENKHORST, P. W., 1987a. Atlas of Victorian Mammals – application and usage. *Abstracts, 33rd Scientific Meeting, Australian Mammal Society*, May 1987, p. 15.

MENKHORST, P. W., 1987b. Working list of Victorian mammals: Second (revised) edition. *Arthur Rylah Institute Technical Report Series* No. 50 (National Parks and Wildlife Division, Victoria).

MENKHORST, P. W. & SEEBECK, J. H., 1990. The distribution and conservation status of bandicoots in Victoria. In *Bandicoots and Bilbies*, Surrey Beatty & Sons, Sydney. Seebeck, J. H., Brown, P. R., Wallis, R. L. & Kemper, C. M. (eds), 51–60.

MITCHELL, T. L., 1839. *Three Expeditions into the Interior of Eastern Australia:* with Descriptions of the Recently Explored Region of Australian Felix, and of the Present Colony of New South Wales. (Vol. II: Expedition to the Rivers Darling and Murray, in the Year 1836.) T. & W. Boone, London. [1965 facsimile edition by Libraries Board of South Australia.]

MORGAN, J., 1852. *The Life and Adventures of William Buckley.* Archibald Macdougall, Hobart. [1967 edition, edited by C. E. Sayers; Heinemann, Melbourne.]

MORTON, W. L., 1966. *Notes of a Tour in the Wimmera District (June and July 1861).* National Parks Authority, Victoria.

OGILBY, J. D., 1892. *Catalogue of Australian Mammals with Introductory Notes on General Mammalogy.* Australian Museum, Sydney.

PARRIS, H. S., 1950. From Melbourne to the Murray in 1839. (Extracts from the Diary of a Pioneer Naturalist, Dr. Edmund Charles Hobson.) *Victorian Naturalist* 66: 183–190, 203–210.

PESCOTT, R. T. M., 1954. *Collections of a Century.* National Museum of Victoria, Melbourne.

PRESLAND, G. (ed.), 1977a. Journals of George Augustus Robinson. January–March 1840. *Records of the Victorian Archaeological Survey* 5: 1–104.

PRESLAND, G. (ed.), 1977b. Journals of George Augustus Robinson. March–May 1841. *Records of the Victorian Archaeological Survey* 6: 1–117.

PRESLAND, G. (ed.), 1980. Journals of George Augustus Robinson. May–August 1841. *Records of the Victorian Archaeological Survey* 11: 1–202.

RANDELL, J. O. (ed.), 1978. *Adventures of a Pioneer, William Lockhart Morton.* Queensberry Hill Press, Carlton.

RAWSON, G., 1946. *Matthew Flinders' Narrative of his Voyage in the Schooner Francis: 1798.* Preceded and Followed by Notes on Flinders, Bass, the Wreck of the Sidney Cove, & C. The Golden Cockerel Press, London.

ROBERTSON, P., BENNETT, A. F., LUMSDEN, L. F., SILVEIRA, C. E., JOHNSON, P. G., YEN, A. L., MILLEDGE, G. A., LILLYWHITE, P. K. & PRIBBLE, H. J., 1989. Fauna of the Mallee study area, north-western Victoria. *Arthur Rylah Institute Technical Report Series* No. 87. Department of Conservation, Forests and Lands, Victoria.

SCARLETT, N., 1969. The Bilby, *Thylacomys lagotis*, in Victoria. *Victorian Naturalist* 86: 292–294.

SEEBECK, J. H., 1984. Mammals of the Western Plains or, Where have all the wombats gone? In *The Western Plains — a Natural and Social History*. Australian Institute of Agricultural Science, Melbourne. Conley, D. & Dennis, C. (eds), 39–53.

SEEBECK, J. H. & BESTE, H. J., 1970. First record of the New Holland Mouse (*Pseudomys novaehollandiae* [Waterhouse, 1843]) in Victoria. *Victorian Naturalist* 87: 180–187.

SEEBECK, J. H. & JOHNSTON, P. G., 1980. *Potorous longipes* (Marsupialia: Macropodidae); a new species from eastern Victoria. *Australian Journal of Zoology* 28: 119–134.

SHILLINGLAW, J. J. (ed.), 1879. *Historical Records of Port Phillip: the First Annals of the Colony of Victoria*. Government Printer, Melbourne.

STOKES, J. L., 1846. *Discoveries in Australia, with an Account of the Coasts and Rivers Surveyed during the Voyage of the HMS Beagle 1837–43*. Vol. 1. Bone, London. [1969 facsimile edition by Libraries Board of South Australia.]

TUCKEY, J. H., 1805. *An Account of a Voyage to Establish a Colony at Port Phillip in Bass's Strait, on the south coast of New South Wales, in His Majesty's Ship Calcutta, in the years 1802-3-4*. Longman, Hurst, and Orme, London.

VOLLETH, M. & TIDEMANN, C. R., 1989. Chromosome studies in three genera of Australian vespertilionid bats and their systematic implications. *Zietschrift fur Saugetierkunde* 54: 215–222.

VOLLETH, M. & TIDEMANN, C. R., 1991. The origin of the Australian Vespertilioninae bats, as indicated by chromosomal studies. *Zeitschrift fur Saugetierkunde* 56: 321–330.

WAKEFIELD, N. A., 1960. Recent mammal bones in the Buchan district — 2. *Victorian Naturalist* 77: 228–240.

WAKEFIELD, N. A., 1963. Mammals of Victoria. *Victorian Year Book* 77: 1–24.

WAKEFIELD, N. A., 1966. Mammals of the Blandowski expedition to north-western Victoria, 1856–57. *Proceedings of the Royal Society of Victoria* 79: 371–391.

WAKEFIELD, N. A., 1972. Palaeoecology of fossil Mammal assemblages from some Australian caves. *Proceedings of the Royal Society of Victoria* 85: 1–26.

WAKEFIELD, N. A. & WARNEKE, R. M., 1963. Some revision in *Antechinus* (Marsupialia) — 1. *Victorian Naturalist* 80: 194–219.

WAKEFIELD, N. A. & WARNEKE, R. M., 1967. Some revision in *Antechinus* (Marsupialia) — 2. *Victorian Naturalist* 84: 66–99.

WARNEKE, R. M., 1963. A list of the mammals occurring or recently recorded in Victoria. Mimeo. Papers prepared for 13th Annual Conference of Fisheries and Wildlife Officers. Fisheries and Wildlife Department, Victoria.

WEATHERALL, F. A., 1826. Dispatch to Governor Darling from HMS Fly, 27 December 1826. In Gullick, W. A. (ed.), 1922, *Historical Records of Australia*. Ser. 3, v. 5. Government Printer, Sydney, 831–834.

(WHEELWRIGHT, H. W.), 1861. *Bush Wanderings of a Naturalist; or, notes on the Field Sports and Fauna of Australia Felix*. Routledge, Warne and Routledge, London.

WILLIS, J. H. & SKEWES, C. 1., 1955. Robert Brown's Bass Strait Journal of April/May 1802. *Muelleria* 1: 46–51.

MORPHOLOGICAL VARIATION IN THE SPIONID POLYCHAETE
BOCCARDIA PROBOSCIDEA

David A. Petch*

Department of Zoology, University of Melbourne, Parkville, Victoria 3052, Australia
*Current address: Biosis Research Pty Ltd, 322 Bay Street, Port Melbourne, Victoria 3207, Australia

Petch, D. A., 1995:07:31. Morphological variation in the spionid polychaete *Boccardia proboscidea*. *Proceedings of the Royal Society of Victoria* 107 (1): 25–30. ISSN 0035-9211.
Specimens of the spionid polychaete *Boccardia proboscidea* from throughout its known geographic range were examined and compared. Despite the wide ecological variation between populations of *B. proboscidea*, no variation in adult morphology was found which would allow separation of specimens from temperate waters. Previously described specimens of *B. proboscidea* from arctic and tropical waters were, however, found to be separate.

THE SPIONID POLYCHAETE *Boccardia proboscidea* Hartman, 1940 has been reported from a wide range of habitats over a wide geographic area around the Pacific basin (Blake & Kudenov 1978). The reported distribution of this species extends along the Pacific coast of North America from Panama to the Bering Sea, surrounding the islands of northern Japan, and along the southern coast of Australia.

The ecological range of *B. proboscidea* has also been reported to be wide. This species has been found: burrowing in soft rock (Hartman 1940); living in crevices on an exposed rock platform (Hartman 1940); amongst coralline algae (Woodwick 1963); in the centre of a colony of the tubeworm *Galeolaria caespitosa* Savigny, 1818 (Hutchings & Turvey 1984); on a sandy beach (Fauchald 1977); among barnacles on jetty pilings (Woodwick 1963); on an intertidal mudflat (Woodwick 1963); in seagrass beds (Imajima & Hartman 1964; Hartmann-Schröder 1982); and, in high densities around major sewage outfalls (Poore & Kudenov 1978; Dorsey 1982; Petch 1989).

The ecological requirements of almost all of the Australian populations of *B. proboscidea* appear dissimilar to those of other populations overseas. In south-eastern Australia, almost all *B. proboscidea* have been found in large aggregations adjacent to major sewage outfalls (Petch 1989). Only one large colony of this species, at Elliston in South Australia (Hutchings & Turvey 1984), and a few scattered individuals have been discovered living away from areas of organic enrichment (Petch 1989). This contrasts with the records of *B. proboscidea* from Japan and North America where only one population has been recorded in an area subject to organic enrichment (Dorsey et al. 1981).

Considering the reported large ecological and geographic ranges of this species and its substantial differences in ecological requirements, at least between North America and Australia, some doubt must exist as to whether populations currently referred to as *B. proboscidea* represent more than one species. The purpose of the present study was to determine whether there was any morphological or morphometric evidence to suggest that this is indeed the case.

MATERIALS AND METHODS

The specimens of *Boccardia proboscidea* examined for the present study were collected from throughout the known geographic and ecological ranges of the species. Sources of museum specimens are indicated by the following abbreviations: USNM, Smithsonian Institution, Washington D.C.; AHF, Allan Hancock Foundation, Los Angeles; and ZMH, Zoologisches Museum Hamburg.

Examination of museum specimens was conducted using light microscopy. Additional material was also examined using scanning electron microscopy (SEM). Specimens for the latter were fixed in 4% formaldehyde then transferred to 70% ethanol, dehydrated through an alcohol series, critical-point dried, coated with gold, and examined with a Philips 505 SEM.

Characters previously used to delineate species in *Boccardia* have included the shape of the caruncle, the distribution of branchiae, the number and type of heavy spines on setiger five, the presence of notosetae on setiger one and the shape of the pygidium (Blake & Woodwick 1971). All specimens examined in the current study were very similar when comparisons were made using the above characters. A more detailed examination of the morphometry of *B. proboscidea* was thus undertaken to establish whether other characters

or combinations of characters could be useful in establishing morphological differences to coincide with ecological differences.

Multivariate discriminant analysis using Systat software (Wilkinson 1990) was used to compare all specimens. Several morphometric measurements were made and these were reduced to a series of ratios to simplify the analysis and to accommodate specimen size, particularly the syntypes which were generally larger than most of the other material. No correlation was found between size and any of the character ratios used in the discriminant analysis. The ratios examined were:

1. Width of setiger five vs. length of the caruncle (ABRAT).
2. Width of setiger five vs. number of hooded hooks on setiger seven (AH7RAT).
3. Number of hooded hooks on setiger seven vs. the number of hooded hooks on setiger sixteen (HHRAT).
4. Number of brush-topped setae on setiger five vs. number of hooded hooks on setiger seven (HHBTRAT).

These ratios were selected to give a representation of the morphometry of the anterior end of *Boccardia proboscidea*. Because of the large number of incomplete specimens examined only characters from the anterior portion of the worm were used.

Specimens were allocated to one of five localities in the discriminant analysis. These were: A, temperate waters of North America; B, southern Australia; C, northern Japan; D, Panama; E, Alaska.

Characters requiring examination of complete specimens were treated in separate analyses. These analyses compared only the North American material with the Australian material as the small numbers of complete specimens from other populations precluded their inclusion. Comparisons using analysis of covariance were made between the total number of setigers and the width of setiger five, and the total number of setigers and the number of hooded hooks on setiger seven. A t-test was used to determine whether there was any difference between populations in the proportion of setigers that bore branchiae. For this analysis the proportional data were normalised using an arsine ($\sqrt{p}$) transformation.

Family SPIONIDAE

Boccardia proboscidea Hartman, 1940

non *Polydora californica* Treadwell 1914: 203.
HOMONYM *Spio californica* (Fewkes 1889).

Boccardia proboscidea Hartman 1940: 382.—1941: 299.—1944: 259.—1961: 28.—1969: 95.—Hartman & Reish 1950: 27.—Berkeley & Berkeley 1950: 51.—1952: 17.—Woodwiek 1963: 132.—1977: 347.—Imajima & Hartman 1964: 279.—Fauchald 1977: 47.—Blake & Woodwick 1971: 31.—Blake & Kudenov 1978: 238.

non *Boccardia proboscidea* Carrasco 1974: 186.—1976: 8 [= *B. tricuspa* (Hartman)].

Material examined. Syntypes: Caspar, California (39°25'N,123°48'W), coll. O. Hartman, July 1934. USNM 020217, 10 specimens. *Other material:* U.S.A., locality undetermined, holotype of *Polydora californica* Treadwell, AHF 73254, 1 specimen; Alaska, Bering Sea, St Paul Island (57°05'N,170°15'W), in holdfast with *Fabricia sabella*, coll. W. L. Hahn, 11 March 1911, USNM 24105, 1 specimen; British Columbia, Port Albion, coll. E. & C. Berkeley, 21 May 1945, USNM 40865, 2 specimens; Washington, San Juan Island, False Point (48°30'N, 123°05'W), coll. M. Pettibone, 1937, USNM 45195, 1 specimen; San Juan Archipelago, Brown Island (48°30'N,123°05'W), coll. M. Pettibone, Summer 1937, USNM 45196, 1 specimen; Lopez Island, Flat Point (48°30'N,122°48'W), coll. M. Pettibone, 11 August 1935, USNM 45194, 1 specimen; California, Fort Bragg (39°29'N,123°46'W), O. Hartman, July 1934, USNM 39566, 6 specimens; California, Bodega Lagoon (38°19'N,123°05'W), 15 June 1941, AHF 287, 1 specimen; California, Bodega, (38°19'N,123°05'W), A. Saphire, August 1986, two sites; (a), from the rocky intertidal on an exposed ocean beach; 15 specimens and (b), from a soft sediment in a sheltered embayment, 12 specimens; California, west of Muir Creek, coll. E. & C. Berkeley, 22 July 1959, USNM 40866, 19 specimens; California, Fruitvale Bridge, Lake Merritt, San Fransciseo Bay (37°53'N,122°17'W), coll. O. Hartman, AHF 1447, 3 specimens; California, San Mateo (37°33'N,122°22'W), coll. L. Oglesby, 17 March 1961, USNM 39637, 5 specimens; California, Moss Beach (37°31'N,122°31'W), coll. O. Hartman, November 1932, AHF 3463, 6 specimens, burrowing in sandstone; California, Moss Landing (36°45'N,112°47'W), coll. D. Petch, 10 October 1986, two sites; (a) from amongst barnacles on a pier piling on exposed ocean beach; 20 specimens and (b) from amongst soft sediments on the high intertidal region of the Elkhorn Slough a sheltered estuary 20 specimens; Long Beach, Mouth of the San Gabriel River (48°30'N, 117°06'W), coll. D. Petch & J. Laughlin, 4 October 1986, 12 specimens, soft sand, high intertidal; California, Laguna Beach (33°32'N,117°45'W), coll. O. Hartman, 11 December 1935, AHF 1448, 6 specimens, north of pier in soft blue shale; California, La Jolla (32°50'N, 117°16'W), coll. Velero expeditions, 28 November 1940, AHF 1597, 2 specimens; Mexico, Rosarito, Baja California (32°20'N,117°04'W), coll. Velero Expeditions, AHF 2238, 1 specimen; Descanso (32°14'N,116°58'W), coll. Velero Expeditions, 6 March 1940, rocky intertidal, AHF 7923, 10 specimens; Ensenada (31°53'N,116°35'W), coll. Dawson & Durham, AHF 1516-46, 1 specimen; Panama, Patilla Beach, 3 specimens, collection details in Fauchald (1977); Japan, Shirikishinai, Hokkaido

27(41°49'N,141°12'W), coll. M. Imajima, USNM 45198, 1 specimen; Hokkaido, Shirikishinai (41°49'N,141°12'W), coll. M. Imajima, February 1955, AHF 11095, 3 specimens; Australia, Victoria, Port Phillip Bay, Werribee Sewage Treatment Farm, Murtcaim Main Drain (38°03'S, 144°31'E), coll. D. Petch, January to December 1984, 10 specimens. Intertidal soft sediment adjacent to a major outfall discharging secondarily-treated sewage effluent; Victoria, Port Phillip Bay, Werribee Sewage Treatment Farm, 145 West Main Drain (38°00'S,144°36'E), coll. J. Kudenov, 25 August 1976, 10 specimens. Port Phillip Bay, Werribee Sewage Treatment Farm, 145 West Main Drain, (38°00'S,144°36'E), coll. D. Petch, January to December 1984, 10 specimens. Intertidal soft sediment adjacent to a major outfall discharging secondarily-treated sewage effluent; Victoria, Port Phillip Bay, Werribee Sewage Treatment Farm, 15 East Main Drain (37°59'S, 144°40'E), coll. D. Petch, January to December 1984, 10 specimens. Subtidal soft sediment adjacent to major outfall discharging secondarily-treated sewage effluent; Victoria, Gunnamatta Beach (38°25'S,144°49'E), coll. D. Petch, January to December 1984, intertidal rock platform on exposed ocean beach adjacent to a major outfall discharging secondarily-treated sewage effluent, 10 specimens; South Australia, Elliston (33°37'S, 134°34'E), coll. D. Petch, 3–5 July 1985, amongst coralline algae on a sandstone rock platform and in colonies of the tube worm *Galeolaria caespitosa* encrusting jetty pilings, 20 specimens; Western Australia, Fremantle (32°07'S,115°44'E), G. Hartmann-Schröder, 27 August 1975. Inside fishing port in sand with algae, ZMH P-17041. 6 specimens.

Colour. In life, pale yellow all over. Branchiae bright red. Pygidium white. Sooty pigment laterally alongside caruncle forming two long black lines. Ciliated areas of palps also black in some specimens. Four eyespots slightly anterior to insertion of palps, in pairs with posterior pair slightly more medial than anterior pair. Small amounts of sooty pigmentation variously on other parts of body. In alcohol, worm pale yellow all over with only sooty pigmentation and eyespots retained.

Measurements. Syntypes range from 86 setigers (0.61 mm wide at the fifth setiger) to 149 setigers (1.23 mm). Other North American material ranged from 29 setigers (0.58 mm) to 153 setigers (1.53 mm). The Australian material extended from 37 setigers (0.78 mm) to 101 setigers (1.43 mm), while that from Japan ranged from 0.77 mm across the fifth setiger to 1.10 mm. The only complete Japanese specimen was one of 60 setigers (0.98 mm). The Panamanian specimens ranged from 0.56 to 0.61 mm across setiger five and the incomplete specimen from St Paul Island, Alaska was 4.24 mm wide at setiger five.

Description. Prostomium rounded to weakly incised on anterior margin, extending posteriorly to the posterior margin of setiger three. A thick band of cilia runs down either side of caruncle (nuchal organ). Prostomial palps short, extending posteriorly to between setigers ten to fourteen. Notosetae present from setiger one, absent from setiger five, all notosetae simple capillary with fine denticulations along one edge. Neurosetae from setiger one, structure as for notosetae. Setiger five heavily modified. Heavy spines of setiger five of two types; (a) simple, falcate, and (b) bristle topped. Always one less falcate spine than the number of bristle topped spines. Small fascicle of capillary setae present ventral to larger spines on setiger five. Bidentate hooded hooks present from setiger seven, Small fascicle of capillary setae ventral to the hooded hooks present on setigers 7, 8, 9, and no others. Hooded hooks accompanied anteriorly and ventrally by small bulbous papillae. Relationship between the number of hooded hooks on setiger seven and the total number of setigers, $y = 0.003x + 2.69$ ($r^2 = 0.56$, Standard Error of Estimate $= 0.96$) (range $= 4$ to 10, average number of hooded hooks on setiger $7 = 6.2$). Number of hooded hooks decreases from half way along body to only two to three hooks on the most posterior setigers. Branchiae present from setiger two, absent from setiger five and posterior 10% of setigers. Branchiae do not touch across midline. Relationship between total number of setigers and number of setigers with branchiae: $y = 1.08x - 17.4$, $n = 117$, $r^2 = 0.97$, s.e. $= 5.65$, $p < 0.001$. Pygidium a broad, flat disc of four unequal lobes, dorsal lobes smaller than ventral lobes.

RESULTS

Statistical Analyses. The results of the discriminant analysis are presented in Fig. 1 and Table 1. No discrimination was possible between the Australian (B) or North American populations (A) from temperate waters. The range of A for both factor 1 and factor 2 entirely encompassed the range of populations B, C, and D. Other character combinations were used in the discriminant analysis; however, all gave essentially the same result. The specimen collected from St Paul Island, Alaska (population E) was the only one clearly demonstrated to be different from the other material (Fig. 2).

The specimens from Panama (population D) were not found to be different using the above analysis. However, differences in other taxonomic characters separate these specimens from remaining temperate specimens of *B. proboscidea*. These data were not included in the analysis because they completely dominated the principal factor and thus
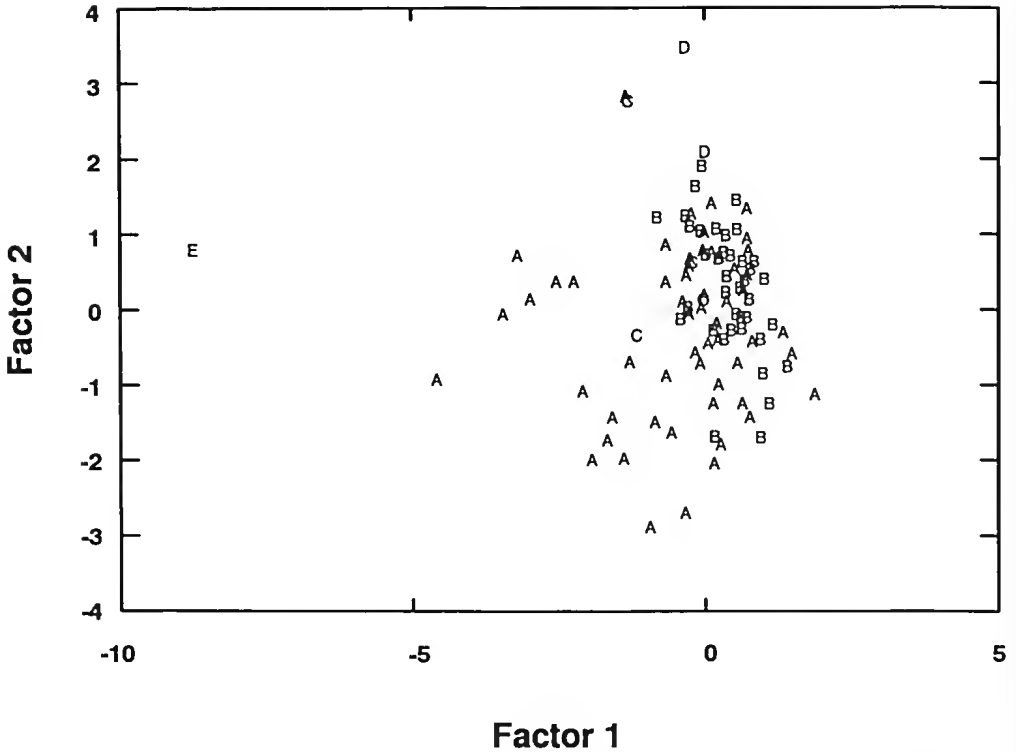
Fig. 1. Distribution of discriminant scores for Factor 1 and Factor 2. Details of the analysis are given in the text. Geographic locations represented are: A, temperate North America; B, Australia; C, Panama; D, Japan; and E, Alaska.

Dependent	Factor			
variable	1	2	3	4
ABRAT	0.193	−0.179	−0.020	1.013
AH7RAT	−1.585	0.789	−0.996	0.079
HHRAT	−0.387	0.884	0.495	0.151
HHBTRAT	0.738	−1.352	1.292	−0.320
Can. corr.	0.667	0.425	0.249	0.112

Table 1. Dependent variable canonical correlations standardised by conditional (within groups) standard deviations. The definitions of the dependent variables are given in the main text.

obscured any differences between the different temperate populations. The additional eharacters are the ratio of brush-topped to falcate setae on setiger five, and the distribution of eapillary neurosetae along the body of the worm. On the Panamanian speeimens the numbers of falcate and brush-topped heavy spines on setiger five are equal, whereas on all other specimens there is invariably one fewer faleate spine than brush-topped spine. The small faseicle of capillary setae that is found only on setigers seven to nine of the temperate water speeimens was absent on the Panamanian speeimens. On the Alaskan specimen capillary setae were found on all setigers posterior to setiger five.

Analysis of the relationship between the total length of the worm and the width of setiger five revealed no signifieant differenee between the Australian and North Amcrican spccimens (F = 1.463, d.f. = 1, 76, P = 0.230). Similarly there was no significant difference in the proportion of the body that bore branehiae (t = 1.88, d.f. = 76, P = 0.239) and no differencc between the numbers of spines on setiger five and total lcngth (F = 1.308, d.f. = 1, 81, P = 0.251) nor between thc number of hooded hooks on setiger seven and total length (F = 1.279, d.f. = 1, 79, P = 0.256).

DISCUSSION

All specimens examined conformed to the original description of *Boccardia proboscidea*. Specimens from Chile described as *B. proboscidea* by Carrasco (1974, 1976) were not examined as Blake & Kudenov (1978) considered Carrasco's reports to refer to *B. tricuspa*. The redescription of *B. proboscidea* divides the specimens examined during this study into three different populations. These are: *B. proboscidea* from temperate waters with a small bundle of capillary setae ventrally on setigers 7, 8, and 9, and ventrally on setiger 5, and with one less falcate seta than brush-topped setae on setiger 5; specimens from Panama with no bundles of capillary setae and a even number of falcate and brush-topped setae on setiger 5; and the single Alaskan specimen with small bundles of capillary setae and an uneven number of heavy spines on setiger 5. The Panamanian material was also distinguished by the ratio of brush-topped spines to heavy spines on setiger five. The Alaskan material was distinguished by the general appearance of the anterior end of the worm (Fig. 1) as well as by the arrangement of the capillary setae. The Alaskan and Panamanian populations probably represent distinct species, but they are not described here due to the poor condition of the material.

The specimens collected from waters between 30° and 50°of latitude exhibited no variation in the adult morphology that would allow distinction between specimens originating from different geographic locations. Despite the collection of specimens from such very different habitats as soft sediments in highly enriched areas surrounding sewage outfalls on sheltered coasts to boring in sandstone on a high-energy surf beach, none of the statistical analyses permitted separation of populations. The choice of characters and statistical techniques used was able to separate *B. proboscidea* from closely related species such as *B. berkelyorum* Blake & Woodwick, 1971 but was unable to detect any inconsistency between populations of *B. proboscidea*.

The results indicate that the adult morphology of *B. proboscidea* from temperate waters surrounding the Pacific basin is remarkably constant. No evidence was found to indicate the presence of more than one species and all adult specimens conform to the type material.

ACKNOWLEDGEMENTS

REFERENCES

BLAKE, J. A. & KUDENOV, J. D., 1978. The Spionidae (Polychaeta) from southeastern Australia and adjacent areas with a revision of the genera. *Memoirs of the National Museum of Victoria* 39: 171–280.

BLAKE, J. A. & KUDENOV, J. D., 1981. Larval development, larval nutrition and growth for two *Boccardia* species (Polychaeta:Spionidae) from Victoria, Australia. *Marine Ecology—Progress Series* 6: 175–182.

BLAKE, J. A. & WOODWICK, K. H., 1971. A review of the genus *Boccardia* Carazzi (Polychaeta: Spionidae) with descriptions of two new species. *Bulletin of the Southern California Academy of Science* 70: 31–42.

CARRASCO, F. D., 1974. Spionidae (Polychaeta) provenientes de la Bahia de Concepcion y lugares adyacentes. *Bolletin de la Sociedad de biologiá de Concepción* 48: 185–201.

CARRASCO, F. D., 1976. Larvas de la familia Spionidae (Polychaeta) en el plancton de la Bahia de Conception, Chile. *Gayana Instituto de Biologia e Zoologia* 38: 1–63.

DORSEY, J. H., 1982. Intertidal community offshore from the Werribee Sewage Treatment Farm: an opportunistic infaunal assemblage. *Australian Journal of Marine and Freshwater Research* 33: 45–54.

DORSEY, J. H., GREEN, K. D. & ROWE, R. C., 1981. Effects of sewage disposal on the polychaetous annelids at San Clemente Island, California. In *Waste Disposal in the Oceans, Minimising Impact, Maximising Benefits*, D. F. Soule & D. Walsh, eds, Westview Press, Boulder, Colorado, 19–39.

FAUCHALD, K., 1977. Polychaetes from intertidal areas in Panama, with a review of previous shallow-water records. *Smithsonian Contributions to Zoology* 221: 1–81.

HARTMAN, O., 1940. *Boccardia proboscidea*, a new species of spionid worm from California. *Journal of the Washington Academy of Sciences* 30: 382–387.

HARTMANN-SCHRÖDER, G., 1982. Die Polychaeten der subtropisch-antiborealen Westküste Australiens (zwischen Cervantes im Norden und Cape Naturaliste im Süden). *Mitteilungen aus dem Hamburgisches Zoologiches Museum und Institut* 79: 51–118.

HUTCHINGS, P. A. & TURVEY, S. P., 1984. The Spionidae of South Australia (Annelida/Polychaeta). *Transactions of the Royal Society of South Australia* 108: 1–20.

IMAJIMA, M. & HARTMAN, O., 1964. The polychaetous annelids of Japan. 1–11. *Allan Hancock Foundation, Occasional Papers* 26: 1–452.

POORE, G. C. B. & KUDENOV, J. D., 1978. Benthos around an outfall of the Werribee sewage treatment farm. *Australian Journal of Marine and Freshwater Research* 29: 157–167.

PETCH, D. A., 1989. Variation in the Spionid polychaete *Boccardia proboscidea* Hartman 1940. Unpublished Ph.D thesis, University of Melbourne. 136 p.

WILKINSON, L., 1990. *SYSTAT: The System for Statistics*. Systat Inc., Evanston, Illinois, U.S.A. 678 p.

WOODWICK, K. H., 1963. Comparison of *Boccardia columbiana* Berkeley and *Boccardia proboscidea* Hartman (Annelida, Polychaeta). *Bulletin of the Southern California Academy of Sciences* 62: 132–139.

EMERSION OF MURRAY CRAYFISH, *EUASTACUS ARMATUS* (DECAPODA:PARASTACIDAE), FROM THE MURRAY RIVER DUE TO POST-FLOOD WATER QUALITY

L. J. McKinnon

Department of Conservation and Natural Resources, Kaiela Fisheries Research Station, P.O. Box 1226, Shepparton, Victoria 3630

McKinnon, L. J., 1995:07:31. Emersion of Murray crayfish, *Euastacus armatus* (Decapoda: Parastacidae), from the Murray River due to post-flood water quality. *Proceedings of the Royal Society of Victoria* 107 (1): 31-37. ISSN 0035-9211.

Mass emersion of Murray crayfish (*Euastacus armatus*) from the Murray River near Barmah occurred following extensive flooding in Barmah and Millewa Forests in 1992. Crayfish walked out of the river and were observed clinging to the riverbank and partially inundated timber. This behaviour was observed after floodwater, which had been stagnant on the Barmah/Millewa Forest floodplain, had drained from the forest and into the Murray River. At the time of the emersion dissolved oxygen concentrations were below 2.0 mg/L throughout the water column and diel range was from 11-19% saturation.

THE MURRAY, or spiny freshwater crayfish (*Euastacus armatus*) von Martens is present throughout a large proportion of the Murray–Darling Drainage Division incorporating Victorian and southern New South Wales tributaries (Riek 1969) where its geographic range extends over 800 km east–west and 450 km north–south (Morgan 1986). *E. armatus* is now thought to be locally extinct in the Murray River downstream of Mildura (Barker 1990) including South Australia (Zeidler 1982; Geddes et al. 1993) and its distribution in general appears to have declined since European settlement (Barker 1990). The conservation status of *E. armatus* is currently defined as 'Indeterminate' due to '*some populations of the species being at risk from a combination of fishing and other environmental factors*' (Horwitz 1990). Habitat degradation is thought to be the greatest threat to Murray crayfish in Victoria (Barker 1990), however Lintermans & Rutzou (1991) suggest overfishing as the major cause of the decline of Murray crayfish in the ACT. The biology and behaviour of most species of *Euastacus* including *E. armatus* is not well understood (Barker 1990).

Tolerance to various water quality factors have been examined in a number of parastacids (Newcombe 1973; Mills & Geddes 1980; Morrissy et al. 1984) and Unestam (1975) identified the potential for disease to decimate spiny crayfish populations. Although there is limited information available on water quality requirements of Murray crayfish in the species' natural environment (Geddes 1990) they have however been found to be unable to maintain an adequate respiratory rate under hypoxic conditions (Barley 1983; Bezzobs 1988). Geddes et al. (1993) examined the tolerances of Murray crayfish to hypoxia, temperature and salinity.

During flooding, water quality in the Murray River at Barmah is influenced by the changes in water quality which occur in the Barmah/Millewa Forest; a large (60 000 ha), predominantly red gum (*Eucalyptus camaldulensis*), forest (Bren 1988). Due to the narrow channel width of the Murray River between Barmah and Millewa Forests, flooding occurs at relatively low river flows (Dexter et al. 1986). Flooding in the Barmah/ Millewa Forest is often widespread and may last for several months, throughout spring and into summer.

Prior to the regulation of the River Murray, Barmah/Millewa Forest was subject to large-scale flooding with much of the floodplain inundated for up to 24 months and 1-9 months on average in winter and spring (Bren 1987). Under current flow regimes, forest flooding is generally less frequent, less extensive and of shorter duration than under natural conditions (Dexter et al. 1986). The flood event which occurred in Barmah/ Millewa Forest during 1992 however, could be viewed as having been more typical of a reasonably large scale flood under natural conditions. Flooding peaked in Barmah Forest during the last week in October 1992 in response to high flows in the Murray River downstream of Tocumwal and floodwaters receded from Barmah and Millewa Forests, into the Murray River during November and December.

During the recession of floodwaters into the Murray River from the Barmah and Millewa Forests during December 1992 and January 1993, large numbers of Murray crayfish began walking

out of the Murray River between Barmah and the Goulburn River Junction, a distance of approximately 25 km (Fig. 1). The water in the Murray River at this time was extremely dark in colour, a feature attributable to large quantities of dissolved organic matter (Meyer 1990), which impart a yellow-brown colour to the water (Gjessing 1976) giving rise to the term 'blackwater'. Blackwater rivers are present in many parts of the world, particularly tropical areas (Janzen 1974; Meyer 1990) and are typically deficient in oxygen (Janzen 1974). Episodic blackwater events have been observed in temperate mainland Australian rivers on previous occasions (Richardson 1981; Morison 1989) and, in these instances, occurred during the recession of large floods. Murray crayfish have been observed leaving the water during blackwater events following extensive flooding in the Murray River on a number of occasions in previous years (M. Moor, Department of Conservation and Natural Resources, pers. comm.)

and in the Goulburn River near Shepparton (B. Simpson, pers. comm.) and in the Murrumbidgee River (B. Jonassen, pers. comm.). Little information is available on the changes in water quality that occur during such events.

Major changes in water quality often occur with floods (Cullen et al. 1978; Beer et al. 1981; Hart et al. 1987, 1988), although many studies have only documented the changes in electrical conductivity, pH, concentrations of suspended solids, ions, trace metals, nutrients and sediment chemistry. There is little published information on changes in dissolved oxygen and concentrations of dissolved organic material associated with flood events in the Murray–Darling Basin. This paper documents a behavioural response in *E. armatus*, describes the nature of the emersion and investigates water quality as an explanation for the behaviour. Water quality is also discussed as a factor possibly affecting the abundance and distribution of *E. armatus*.
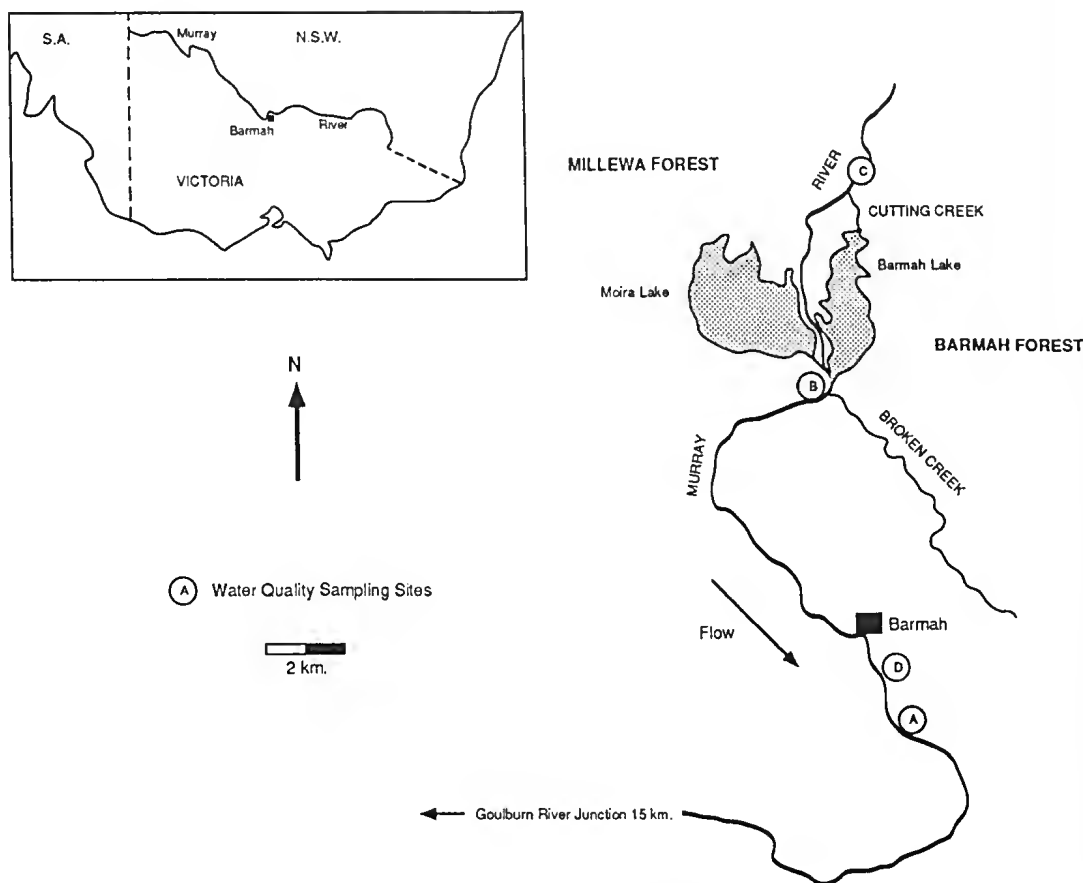
Fig. 1. Map of the Murray River indicating water quality sampling sites.

METHODS

Water quality monitoring sites were chosen to include sites at and upstream of the areas where the emersion of *E. armatus* was observed, and one site where water quality was apparently unaffected by flooding and no crayfish emersion was observed.

On 18 December 1992, water samples were collected downstream of Barmah in the area where the greatest emersion was occurring (site A) and upstream of Barmah where no crayfish emersion was observed (sites B and C) (Fig. 1). Previous fish surveys in the vicinity of sites B and C indicate that Murray crayfish are present at or near these sites (McKinnon, unpubl. data). Water samples for colour and turbidity analysis were collected in 1 L plastic bottles, those for analysis for tannins and lignins collected in 500 mL Pyrex bottles and those for analysis for phenolic compounds in 2.5 L glass Winchester bottles containing 20 mL of 50% w/v sulphuric acid and 2.5 g cupric sulphate (RWC 1988). All water samples were taken at the water surface and immediately stored at 4°C. Water samples were analysed within 48 h at the Rural Water Corporation's State Water Laboratories using standard methods (RWC 1988). In addition, in situ measurements of dissolved oxygen, electrical conductivity, temperature using a TPS 90FL Datalogger, and pH using an Orion 250A model pH meter were made.

On 7 January a TPS 90FL Datalogger was installed in a backwater area on the Murray River (site D, Fig. 1) where crayfish were observed leaving the water in order to monitor the diel changes in dissolved oxygen, temperature, electrical conductivity and pH. Maximum depth at site D was 2.1 m and datalogger probes were fixed at 0.5 m from the bottom. Readings were taken hourly for 5.5 days.

By 21 January 1993, the emersion of crayfish appeared to have ceased and water sampling for colour, turbidity, tannins and lignins and phenols and in situ measurement of dissolved oxygen, temperature, pH and electrical conductivity were repeated at sites A, B and C.

RESULTS

Water quality factors that exhibited the greatest differences between the blackwater sites (sites A and B) and the non-blackwater site (site C) on 18 December, when crayfish were observed leaving the water, were dissolved oxygen and turbidity (Table 1). These were higher at site C and tannins and lignins were slightly lower at this site. Electrical conductivity, pH, colour and phenolic compounds were generally of similar magnitude at all sites.

During the crayfish emersion, water quality factors measured at both blackwater sites (A and B), were of similar magnitude, with the exception of dissolved oxygen (Table 1). Dissolved oxygen at site A, where the emersion was occurring, was 1.8 mg/L, almost half that measured at site B, where no emersion was observed, and one-quarter that measured at site C where neither blackwater nor crayfish emersion was observed (Table 1). Turbidity and pH were lower at sites A and B than at site C and electrical conductivity and levels of tannins and lignins were not significant at sites A and B. At site D dissolved oxygen saturation ranged from just over 19% during the late afternoon to less than 11% in the morning during the

	Crayfish emersion and blackwater observed. Site A (time measured: 1400 h)			Blackwater and no crayfish emersion observed. Site B (time measured: 1510 h)			No crayfish emersion or blackwater observed. Site C (time measured: 1555 h)	
	Mean	s.e.	n	Mean	s.e.	n	Mean	n
Dissolved oxygen (mg/L)	1.8	0	3	3.5	0	2	7.2	1
Temperature (°C)	21.5	0	3	22.0	0	2	22.5	1
pH	6.8	0	3	6.7	0	2	7.5	1
Electrical conductivity (μS/cm)	76.3	0.3	3	82.5	2.5	2	61.0	1
Colour (Pt/Co units)	65.0	0	3	82.5	5.3	2	55.0	1
Turbidity (NTU)	13.0	0.5	3	11.9	5.0	2	43.0	1
Tannins and lignins (mg/L)	1.37	0.03	3	1.55	0.11	2	1.0	1
Phenols (mg/L)	0.006	0.002	3	0.007	0.004	2	0.009	1

Table 1.   Water quality factors measured during the period of Murray crayfish emersion, 18/12/1992.

period 8–12 January 1993, while crayfish emersion was still occurring (Fig. 2). During this period pH exhibited apparently normal diel fluctuations but did not reach considerably extreme levels (Fig. 2). Electrical conductivity showed a gradual increase at site D between 8 and 12 January (Fig. 2) as the water level in the Murray River was dropping.

On 21 January dissolved oxygen at sites A and B had incrcased to levels approximating that recorded at site C and most other water quality factors measurcd were of similar value at all sites (Table 2). Electrical conductivity, turbidity and concentrations of phenols wcre higher at sitc B on 21 January (Table 2) however these could be attributcd to thc influencc of Broken Creek, which receives irrigation drainage water further upstream in the catchment (Fig. 1).

The hydrograph of the Murray River at Barmah from 1 November 1992 to 31 January 1993 (Fig. 3) indicates the period of observed crayfish emersion. Thc emersion of Murray crayfish began after the floodwaters draining Barmah and Millewa Forests had reached Barmah. This is indicated by a small peak in the hydrograph at Barmah in early Dccember 1992 (Fig. 3). The bulk of the emcrsion occurred during the first 2–3 weeks of the emersion period and it is expected that the
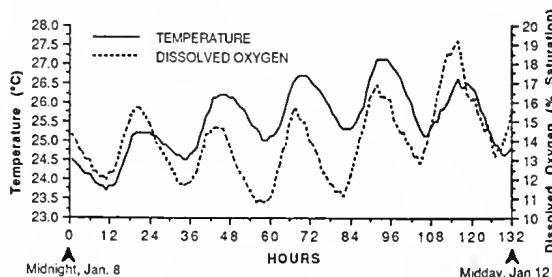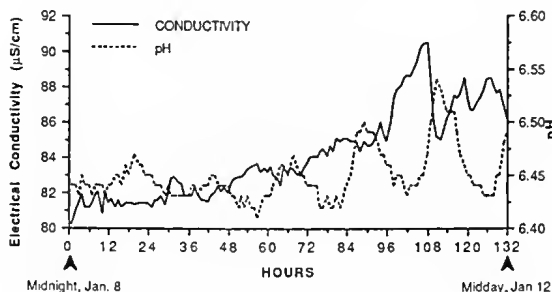
Fig. 2. Diel changes in water quality at site D during the crayfish emersion.
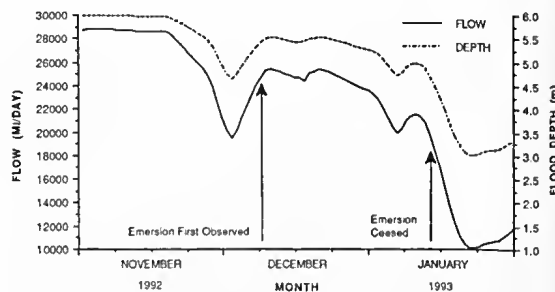
Fig. 3. Hydrograph of the Murray River at Barmah, gauge station 409215, from 1 November 1992 to 31 January 1993.

	Site A (time measured: 1240 h)	Site B (time measured: 1350 h)	Site C (time measured: 1435 h)
Dissolved oxygen (mg/L)	5.6	6.3	6.6
Temperature (°C)	27.8	27.0	27.2
pH	6.9	7.1	7.3
Electrical conductivity (μS/cm)	97.0	112.0	76.0
Colour (Pt/Co units)	65.0	65.0	45.0
Turbidity (NTU)	80.0	83.0	54.0
Tannins and lignins (mg/L)	0.7	0.6	0.4
Phenols (mg/L)	<0.001	0.002	<0.001

Table 2. Water quality factors measured after the period of Murray crayfish emersion, 21/1/1993.

crayfish population in the arca suffcred significant stock depletion due to removal for domestic consumption. An estimated 500 kg of crayfish was removed during the crayfish emersion period (L. Hubbard, pers. comm.). Emersion continued until mid–latc January aftcr which time the forests upstream had ceased to drain and water quality had returned to more favourable levels.

Crayfish were observed walking out of the water and up on to banks along the main river channel and also in backwaters and adjoining billabongs both upstream and downstream of site A from 18 Deccmber until late January. The crayfish moved out of the water and remained at the water's edge, semi-exposcd keeping their gills at the surface of the water. Some animals were observed walking backwards up partially inundated trees, again keeping thcir gills at the surface of the water. Individuals returned to the water when disturbed but re-emerged within 0.5 h. Some animals came out of the water completely but would not move further than about 0.25 m from the water's edge. Over a one-hour observation period at site A from 12.30–13.30 hours on 18 October, 30 individuals were observed behaving in this manner in a 400 m. section of riverbank. The smallest and largest individuals obscrved exhibiting this behaviour were collected and their orbit-carapace length (OCL) measured (25 and 165 mm OCL respectively). The observed behaviour did not appear to be size-specific.

Large schools of Australian smelt (*Retropinna semoni*) and several common carp (*Cyprinus carpio*) were obscrved swimming at the surface of the water at site A. No dead or obviously moribund fish were obscrved, however fish kills due to oxygen depletion during the recession of floodwaters have been previously reported (Richardson 1981; McKinnon & Shepheard 1995).

In backwater areas where emersion was occurring, crayfish were generally solitary and behaved independently of one another. Where crayfish were observed clinging to partially inundated trees and woody debris contiguous to fast flowing water, they were often present in groups of three and four, probably due to the scarcity of refuge sites. In these instances, smallcr animals were sometimes killed by larger individuals crushing them with their chelipeds. Crayfish were generally lethargic and easy to catch, however only a small number of dead animals was observed. It is assumed that more dead crayfish would have been observed were the moribund animals not removed for human consumption.

DISCUSSION

Much of the floodwater, particularly during the latter stages of the flood, was unable to drain away from the floodplain encompassing Barmah and Moira Lakes (Fig. 1) due to the back-up effect of the Goulburn Rivcr which was also in flood, some 45 km downstream. Aerial photography from mid-November indicates the floodwaters at the downstream end of the forests wcre virtually stagnant at that time. This was depicted by a stream of turbid water flowing down the Murray River, meeting the backed-up floodwater and being deflected westwards into Moira Lakc.

As the floodwater remained stagnant, dissolved aquatic humus concentrations would be expected to increase due to the aerobic degradation of organic detritus. This would also be expected to create potentially hypoxic conditions (Welcomme 1979). Dissolved aquatic humus, commonly termed 'tannins and lignins' is further broken down to polyphenolic compounds which are known to be toxic to a wide variety of organisms as they form insoluble complexes with proteins (Janzen 1974). Polyphenolic compounds have been suggested as creating problems with the oxygen exchange surfaces of the gills of fish by binding enzymes on the gills that facilitate respiration (Gehrke 1991; Gehrke et al. 1993). Gchrke et al. (1993) found that this was aggravated in golden perch (*Macquaria ambigua*) larvae exposed to *Eucalyptus camaldulensis* litter leachates under hypoxic conditions. Similar problems may also occur in crayfish exposed to the same conditions. The results from this study indicate that concentrations of tannins and lignins and phenols were similar at sites A, B and C during the period of crayfish emersion. Crayfish emersion was however, only observed at sites A and D at which dissolved oxygen was recorded at concentrations much lower than those recorded at sites B and C.

Geddes et al. (1993) found *E. armatus* held at dissolved oxygen concentrations of 2.1 mg/L for three days did not survive. As dissolved oxygen was recorded at concentrations lower than this for extended periods during the emersion event, it would appear that the effects of hypoxia, possibly combined with the toxic effects of tannins and lignins and phenolic compounds, precipitated the observed behaviour in the crayfish. Studies of the tolerance of a number of *Cherax* species to hypoxia (Barley 1983; Morrissy et al. 1984; Bezzobs 1988) indicate that these species are relatively tolerant of hypoxic conditions. Barley (1983) and Bezzobs (1988) found however, in comparing the tolerance to hypoxia of *C. destructor* with that of *E. armatus*,

that both hyperventilated in hypoxic conditions but *E. armatus* was apparently unable to use anaerobic metabolism to replace aerobic respiration as a source of energy. The inability of *E. armatus* to maintain respiration in hypoxic conditions may explain the emersion of this species from the hypoxic floodwaters in the Murray River and may be an important consideration in the general distribution of the species.

The low dissolved oxygen concentrations recorded at site D from 7–13 January and during the initial sampling on 18 December at site A would be expected to have adverse effects on most fish and crustacean species in the area. The conductivity values observed would not be expected to adversely affect crayfish populations (Mills & Geddes 1980; Geddes et al. 1993), nor would the pH values recorded during this time (Newcombe 1973). Specific pH tolerance levels for *E. armatus* however, are not known. It is unlikely that water temperatures recorded would have contributed to crayfish emersion (Geddes et al. 1993).

The relatively poor water quality in the Murray River due to previously stagnating floodwaters draining Barmah and Millewa Forests appeared to have induced the emersion of *E. armatus*. It is clear that the management of flooding or watering strategies for the Barmah and Millewa Forests must take into account the effects on aquatic biota downstream of these forests as floodwaters recede. It is not expected that the response of Murray crayfish observed downstream of Barmah will occur after every flood. It is suggested that the adverse water quality conditions observed on this occasion were the product of floodwaters stagnating due to the backing-up of water in the main channel caused by extensive flooding of tributaries downstream. This allowed dissolved organic matter to collect in the floodwaters and facilitated the production of potentially toxic polyphenols and hypoxic conditions to a greater degree than that which may occur under continuously flowing flood conditions.

The observed effects of stagnating floodwater on water quality is particularly significant when considering the use of earthen block banks and other small scale works as described by Bren (1990) and Murphy (1990) in Barmah and Millewa Forests to retain floodwater. These works have the potential to create extensive areas of stagnant water. Impeding the steady flow of floodwater through the forests by such means may create similar water quality problems to those described in this paper, possibly with similar adverse consequences for the aquatic biota.

REFERENCES

BARKER, J., 1990. *Spiny Freshwater Crayfish Management Strategy in Victoria.* Fisheries Management Report No. 34. Freshwater Fish Management Branch, Fisheries Division, Victoria. Department of Conservation and Environment. 17 p.

BARLEY, R. J., 1983. A comparison of the responses to hypoxia of the yabbie *Cherax destructor* Clark and the Murray crayfish *Euastacus armatus* (von Martens). BSc (Hons) Thesis (unpublished), University of Adelaide.

BEER, T., YOUNG, P. C., HUMPHRIES, R. B. & BURGESS, J. S., 1982. *Environmental Water Quality. A Systems Study in Tuggeranong Creek and Kambah Pool.* CRES Monograph 5. Australian National University, Canberra. 177 p.

BEZZOBS, T., 1988. A comparison of the respiratory responses of the Murray crayfish *Euastacus armatus* (von Martens) and the yabby *Cherax destructor* (Clark) to maintained hypoxia. BSc (Hons) Thesis (unpublished), University of Adelaide.

BREN, L. J., 1987. The duration of inundation in a flooding river red gum forest. *Australian Forestry Research* 17: 191–202.

BREN, L. J., 1988. Flooding characteristics of a riparian red gum forest. *Australian Forestry* 51(1): 57–62.

BREN, L., 1990. Red Gum Forests. In *The Murray*, N. Mackay & D. Eastburn, eds, Murray–Darling Basin Commission, Canberra, 231–242.

CULLEN, P., ROSICH, R. & BEK, P., 1978. *A Phosphorus Budget for Lake Burley Griffin and Management Implications for Urban Lakes.* Australian Water Resources Council Technical Paper No. 31, Australian Government Printing Service, Canberra, 220 p.

DEXTER, B. D., ROSE, H. J. & DAVIES, N., 1986. River regulation and associated forest management problems in the River Murray red gum forests. *Australian Forestry* 49(1): 16–27.

GEDDES, M., 1990. Crayfish. In *The Murray*, N. Mackay & D. Eastburn, eds, Murray–Darling Basin Commission, Canberra, 303–307.

GEDDES, M. C., MUSGROVE, R. J. & CAMPBELL, N. J. H., 1993. The feasibility of re-establishing the River Murray crayfish, *Euastacus armatus*, in the lower River Murray. *Freshwater Crayfish* 9: 368–379.

GEHRKE, P. C., 1991. Avoidance of inundated flood-plain habitat by larvae of golden perch (*Macquaria ambigua* Richardson): influence of water quality or food distribution? *Australian Journal of Marine and Freshwater Research* 42(6): 707-719.

GEHRKE, P. C., REVELL, M. B. & PHILBEY, A. W., 1993. Effects of river red gum, *Eucalyptus camaldulensis*, litter on golden perch, *Macquaria ambigua*. *Journal of Fish Biology* 43: 265-279.

GJESSING, E. T., 1976. *Physical and Chemical Characteristics of Aquatic Humus*. Ann Arbor Science, Michigan, 120 p.

HART, B. T., DAY, G., SHARP-PAUL, A. & BEER, T., 1988. Water quality variations during a flood event in the Annan River, North Queensland. *Australian Journal of Marine and Freshwater Research* 39: 225-243.

HART, B. T., OTTAWAY, E. M. & NOLLER, B. N., 1987. Magela Creek system, Northern Australia. 1. 1982-83 wet season water quality. *Australian Journal of Marine and Freshwater Research* 38: 261-268.

HORWITZ, P., 1990. *The Conservation Status of Australian Freshwater Crustacea*. Report Series No. 14, Australian National Parks and Wildlife Service, 121 p.

JANZEN, D. H., 1974. Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae. *Biotropica* 6(2): 69-103.

LINTERMANS, M. & RUTZOU, T., 1991. *The Status, Distribution and Management of the Murray Crayfish* Euastacus armatus *in the Australian Capital Territory*. Research Report 6, ACT Parks and Conservation Service, 20 p.

MCKINNON, L. & SHEPHEARD, N., 1995. Factors contributing to a fish kill in Broken Creek. *Victorian Naturalist* 112(2): 93-99.

MEYER, J. L., 1990. A blackwater perspective on riverine ecosystems. *Bioscience* 40(9): 643-651.

MILLS, B. J. & GEDDES, M. C., 1980. Salinity tolerance and osmo-regulation of the Australian freshwater crayfish *Cherax destructor* Clark (Decapoda: Parastacidae). *Australian Journal of Marine and Freshwater Research* 31: 667-676.

MORGAN, G. J., 1986. Freshwater crayfish of the genus *Euastacus* Clark (Decapoda: Parastacidae) from Victoria. *Memoirs of the Museum of Victoria* 47(1): 1-57.

MORISON, S., 1989. *Monitoring of Fish and Fish Habitat During the Trial Flooding of Barmah Forest, December 1988*. Report to the State Working Group on River Murray Wetland and Forest Management. 12 p.

MORRISSY, N. M., CAPUTI, N. & HOUSE, R. R., 1984. Tolerance of marron (*Cherax tenuimanus*) to hypoxia in relation to aquaculture. *Aquaculture* 41: 61-74.

MURPHY, A., 1990. Watering the Millewa Forest. In *The Murray*, N. Mackay & D. Eastburn, eds, Murray-Darling Basin Commission, Canberra, 245-248.

NEWCOMBE, K. J., 1973. The pH tolerance of the crayfish *Parastacoides tasmanicus* (Erichson) (Decapoda, Parastacidae). *Crustaceans* 29(3): 231-234.

RICHARDSON, B. A., 1981. Fish kill in the Belmore River, Macleay River Drainage, NSW, and the possible influence of flood mitigation works. In *Proceedings of the Floodplain Management Conference*, 7-10 May 1980, Canberra. AGPS, Canberra.

RIEK, E. F., 1969. The Australian freshwater crayfish (Crustacea: Decapoda: Parastacidae) with descriptions of new species. *Australian Journal of Zoology* 17: 855-918.

RWC (RURAL WATER COMMISSION OF VICTORIA), 1988. *Chemical Methods, Volume 1. Routine Water Analyses*. Report No. CE25, 2nd Edn. 278 p.

UNESTAM, T., 1975. Defence reactions in and susceptibility of Australian and New Guinean freshwater crayfish to European-crayfish-plague fungus. *Australian Journal of Experimental Biology and Medical Science* 53(5): 349-359.

WELCOMME, R. L., 1979. *Fisheries Ecology of Floodplain Rivers*. Longman, London. 317 p.

ZEIDLER, W. (1982). South Australian freshwater crayfish. *South Australian Naturalist* 56(3): 36-43.

	Crayfish emersion and blackwater observed. Site A (Time measured: 1400h)			Blackwater and no crayfish emersion observed. Site B (Time measured: 1510h)			No crayfish emersion or blackwater observed. Site C (Time measured: 1555h)	
	Mean	s.e.	n	Mean	s.e.	n	Mean	n
Dissolved Oxygen (mg/L)	1.8	0	3	3.5	0	2	7.2	1
Temperature (°C)	21.5	0	3	22.0	0	2	22.5	1
pH	6.8	0	3	6.7	0	2	7.5	1
Electrical Conductivity (µS/cm)	76.3	0.3	3	82.5	2.5	2	61.0	1
Colour (Pt/Co Units)	65.0	0	3	82.5	5.3	2	55.0	1
Turbidity (NTU)	13.0	0.5	3	11.9	5.0	2	43.0	1
Tannins and Lignins (mg/L)	1.37	0.03	3	1.55	0.11	2	1.0	1
Phenols (mg/L)	0.006	0.002	3	0.007	0.004	2	0.009	1

Table 1. Water quality factors measured during the period of Murray crayfish emersion, 18/12/1992.

	Site A (Time measured: 1240h)	Site B (Time measured: 1350h)	Site C (Time measured: 1435h)
Dissolved Oxygen (mg/L)	5.6	6.3	6.6
Temperature (°C)	27.8	27.0	27.2
pH	6.9	7.1	7.3
Electrical Conductivity (µS/cm)	97.0	112.0	76.0
Colour (Pt/Co Units)	65.0	65.0	45.0
Turbidity (NTU)	80.0	83.0	54.0
Tannins and Lignins (mg/L)	0.7	0.6	0.4
Phenols (mg/L)	<0.001	0.002	<0.001

Table 2. Water quality factors measured after the period of Murray crayfish emersion, 21/1/1993.

THE TADPOLE OF *LITORIA SPENCERI* (ANURA : HYLIDAE)

JEAN-MARC HERO[1], GRAEME F. WATSON[2] AND GRAEME GILLESPIE[3]

[1] Wet Tropics Management Authority/Cooperative Research Centre—Tropical Rainforest Ecology and Management/Department of Zoology, James Cook University, Townsville, Queensland 4810
[2] Department of Zoology, University of Melbourne, Parkville, Victoria 3052
[3] Department of Conservation & Natural Resources, Flora and Fauna Branch, Heidelberg, Victoria 3084

The tadpole of the endangered species, *Litoria spenceri*, has a dextral anus, a sinistral spiracle, two rows of teeth in the anterior labium and three rows of teeth in the posterior labium. These morphological features are identifying characteristics for most tadpoles of the genus *Litoria*. The diagnostic characteristics for tadpoles of *Litoria spenceri* include the uniform distribution of chromatophores and the wide oral disc. In East Gippsland, Victoria, tadpoles were found in a range of riparian microhabitats, however, the majority were found in the main streams or connected streamside pools.

LITORIA SPENCERI (Spencer, 1901) is a medium-sized tree frog (up to 60 mm), adult males range between 30 and 40 mm. Dorsal colour in life varies from dark brown to bright green, usually with a warty/spotted appearance. The ventral surface is white and granulated with a yellowish tint under the limbs. All specimens have been found adjacent to fast-flowing rocky streams both east and west of the Great Dividing Range. All known localities are within an altitudinal range between 280 and 1100 metres (Gillespie 1993). Frogs have been found between October and April, and calling males have been heard in October, November and early December (Hero 1990a, 1991; Watson et al. 1991; Gillespie 1993) and February (Gillespie, pers. obs). The seasonal distribution of size classes of frogs and breeding activity (Watson et al. 1991; Gillespie 1993) suggest that eggs are laid in late spring/early summer and tadpoles reach metamorphosis in late summer/autumn.

Historically, *L. spenceri* was known from 11 streams in north-eastern Victoria and at one locality in the Kosciusko region of New South Wales. During the 1980s the species disappeared from many of the localities in which it had previously been encountered. Despite intensive searching between 1989 and 1991, *L. spenceri* could only be located along two streams in Victoria, the Taponga and the Wongungarra Rivers (Watson et al. 1991). Recent surveys have relocated the species in six of the catchments in which it was previously known and along six additional streams (Ehmann et al. 1993; Gillespie 1992, 1993; Gillespie & Hollis, pers. comm.). Another historical record has also been found from the Australian Capital Territory (Osborne et al. 1994).

While *L. spenceri* is now known to be extant in 14 streams, it cannot be located in five streams from which it has previously been recorded, and declines in extent of distribution appear to have occurred along at least four of the other streams (Gillespie 1993; Gillespie & Hollis, pers. comm.). Many of the populations are small and geographically restricted. *Litoria spenceri* is listed as endangered in Australia (ANZECC 1991).

Herein, we present a brief diagnosis and description of the tadpole of *L. spenceri* and the habitats where they have been found in north-eastern Victoria.

METHODS

Tadpoles were collected between January 1990 and April 1994 from streams in north-eastern Victoria as part of intensive surveys for *L. spenceri* (Table 1, Fig. 1).

Tadpoles at two sites, the Wongungarra River and the Taponga River, were identified by growing them to metamorphosis. Tadpoles collected at other localities were identified following confirmation of the identifications at the former two sites. At each collection site, microhabitat was recorded and the presence of tadpoles of other species, as well as any fish, were noted. A brief description of the stream was also compiled. Observations of tadpoles and adults from other sites were also made.

Tadpoles were anaethetised with 1% sodium pentobarbital and preserved in 4% neutral formalin. Measurements were made with the aid of an ocular micrometer fitted to a dissecting microscope. Descriptions are based on living material

and drawings made from tracings of photographs taken using an Olympus JM-Tr dissecting microscope and an Olympus PM-6 photomicrographic camera. Drawings were made of a single representative specimen placed in the Museum of Victoria (NMV D66051).

Habitat and life history notes also are presented to assist identification in the field. These are intended only as a guide and tadpoles could be found in different habitats and months than those given. Caution should be taken with colour descriptions as tadpole colour is often a function of water clarity (Bragg 1957).

Terminology follows Altig (1970) and Hero (1990b) and development stages follow those described by Gosner (1960). For those specimens that have been placed in the Museum of Victoria, museum numbers are presented in Table 1.

Locality	Map and grid reference	Date	Museum of Victoria No.	Gosner stage	Body length (mm)	Total length (mm)	Width of oral disc (mm)	Water body
Big River (Eildon)	8123 205573	19.1.90		25				BW
Wongungarra River	8323 387424	20.2.90		42				CSP
Taponga River	8123 163632	16.2.91		25				FS
	8123 045895	23.2.92	D66048	42	11.6	24.7	*	FS
Goulburn River	8122 385473	21.2.92	D66049	36	12.3	28.1	3.9	FS
Big River	8324 346276	10.3.92	D66050	37	14.7	36.3	4.8	CSP
Mitta Mitta	8324 346276	10.3.92	D66050	38	15.3	36.5	5.0	CSP
	8324 346276	10.3.92	D66050	43	14.7	31.6	*	CSP
	8324 339292	5.3.92	D66051	36	14.9	35.7	4.4	CSP
	8324 339292	5.3.92	D66051	38	15.1	35.8	5.1	CSP
	8324 339292	5.3.92	D66051	38	15.2	36.7	5.2	CSP
	8324 339292	5.3.92	D66051	38	15.3	37.5	5.2	CSP
	8324 339292	5.3.92	D66051	42	14.0	30.5	3.8	CSP
Snowy Creek	8324 387424	12.3.92	D66052	43	15.3	20.7	*	FS
	8324 387424	12.3.92	D66052	46	16.4	16.4	*	PB
Still Creek	8123 040899	24.1.94		28	7.5	18.1	2.4	FS
	8123 040899	24.1.94		28	8.5	19.5	2.5	FS
Black River	8122 389470	25.1.94		37	14.3	31.7	4.0	ISP
	8122 389470	25.1.94		36	14.1	31.0	4.3	ISP
	8122 388468	25.1.94		33	11.7	25.8	3.3	FS
	8122 388468	25.1.94		36	15.8	32.2	4.5	FS
	8122 388468	25.1.94		32	10.5	24.4	3.5	FS
	8122 388468	25.1.94		35	13.3	30.3	4.2	FS
	8122 388468	25.1.94		36	15.8	34.4	4.5	FS
	8122 388468	25.1.94		36	14.3	33.4	4.4	FS
	8122 388468	25.1.94		35	13.9	31.4	4.6	FS
	8122 388468	25.1.94		34	12.1	26.6	3.6	FS
	8122 390467	25.1.94		37	14.9	36.1	4.7	FS
	8122 390467	25.1.94		36	15.0	32.5	4.8	FS
	8122 390467	25.1.94		35	13.9	30.1	4.5	FS
	8122 391465	25.1.94		36	14.6	32.6	4.5	CSP
	8122 391465	25.1.94		36	14.0	31.2	4.5	CSP
	8122 391465	25.1.94		35	12.4	28.1	4.2	CSP
	8122 391465	25.1.94		35	13.2	28.3	3.9	CSP
	8122 391465	25.1.94		35	15.6	32.7	4.7	CSP
	8122 391465	25.1.94		35	15.0	28.8	4.5	CSP
Bogong Creek	8525 126865	10.4.94	not collected	42	17.2	42.0	5.3	CSP

* Mature tadpole with reduced oral disc.

Table 1. Localities and dates of collection, Museum of Victoria number (where available), microhabitat, Gosner stage and size of specimens examined in this study. Habitats are abbreviated as follows: CSP — connected stream side pool; BW — backwater of main stream; FS — flowing stream; ISP — isolated stream side pool; PB — pebble bank. Map and grid references are based on Australia 1:100 000 map series with the map number given before the six-digit grid reference.
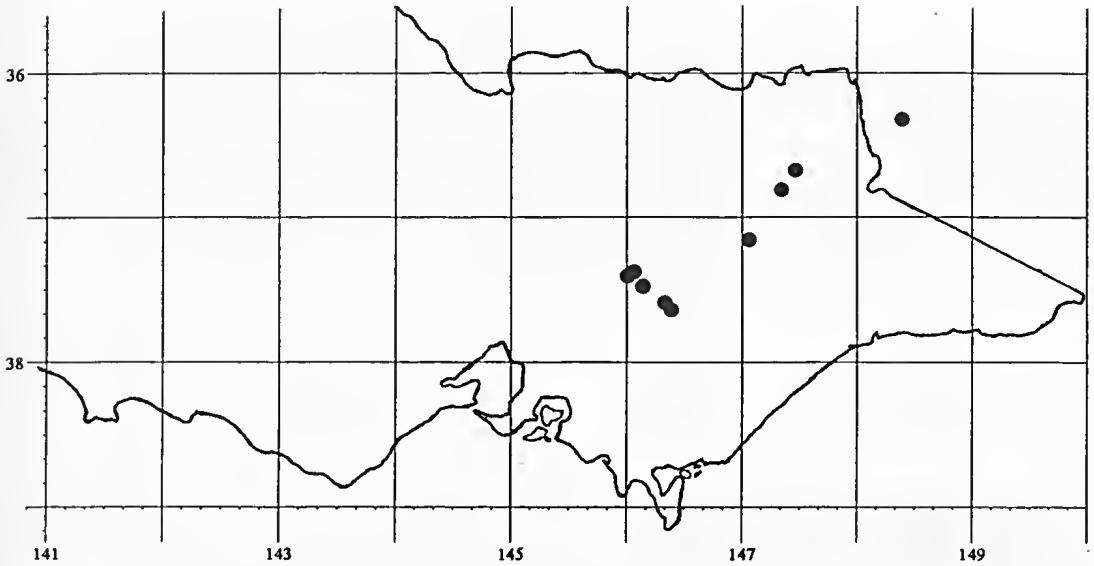
Fig. 1. Localities where tadpoles of *Litoria spenceri* were encountered in this study. (Source: Atlas of Victorian Wildlife.)

RESULTS AND DISCUSSION

Tadpole description (Fig. 2)

The anus is dextral and the spiracle sinistral. Eyes are dorsolateral. The oral disc is large; papillae have a wide anterior gap. There are two rows of labial teeth in the anterior labium and three in the posterior labium. Median gaps are present in the second anterior and the first posterior tooth rows, however, each side of the second anterior tooth row sometimes overlap at the midline as indicated in Fig. 2C.

The body is dark brown above with densely scattered fine silver and gold chromatophores that extend down the tall musculature and fins. Darkly pigmented, but discernible spots are scattered over the dorsum. The lateral body wall has a uniform dense scattering of fine silver chromatophores; the ventral body wall is transparent with scattered fine silver chromatophores extending onto the sides and covering the ventral surface. In life, the blood-filled heart and gills as well as coiled intestine are clearly visible through the ventral body wall. The tail fins are transparent with scattered melanophores; the tail is rounded to subacuminate. The body is streamlined with dorsolateral eyes more or less flush with body.

Measured tadpoles varied in length from 7.5 mm (Gosner stage 28) to 42 mm at Gosner stage 42 (Table 1). A newly metamorphosed juvenile had a body length of 16.4 mm (Table 1).

Calling males have been heard in October, November and early December. Tadpoles were observed between mid-January and early April and newly metamorphosed individuals have been recorded as early as the beginning of February. This suggests that tadpole development takes between two and four months during the summer months.

Habitat

Tadpoles of *L. spenceri* were found in a wide range of riparian microhabitats: connected stream-side pools; backwaters in bedrock pools; directly in streams; and isolated streamside pools (Table 1). The majority of tadpoles were found directly in the main streams or connected stream side pools. Tadpoles were generally observed on the stream bed or along the water edge; grazing or resting on a range of substrates (rock, sand, leaf litter, algae and detritus, and amongst pebbles). Tadpoles were only located in an isolated stream side pool on one occasion (two individuals). This was a bed rock pool which may have become isolated after tadpoles had moved into it. Tadpoles generally occurred in relatively calm or still waters; however this may reflect a bias in sampling, which was predominantly by visual observation. Many tadpoles were located adjacent to rapid water and on one occasion swam into a swift channel to avoid capture.
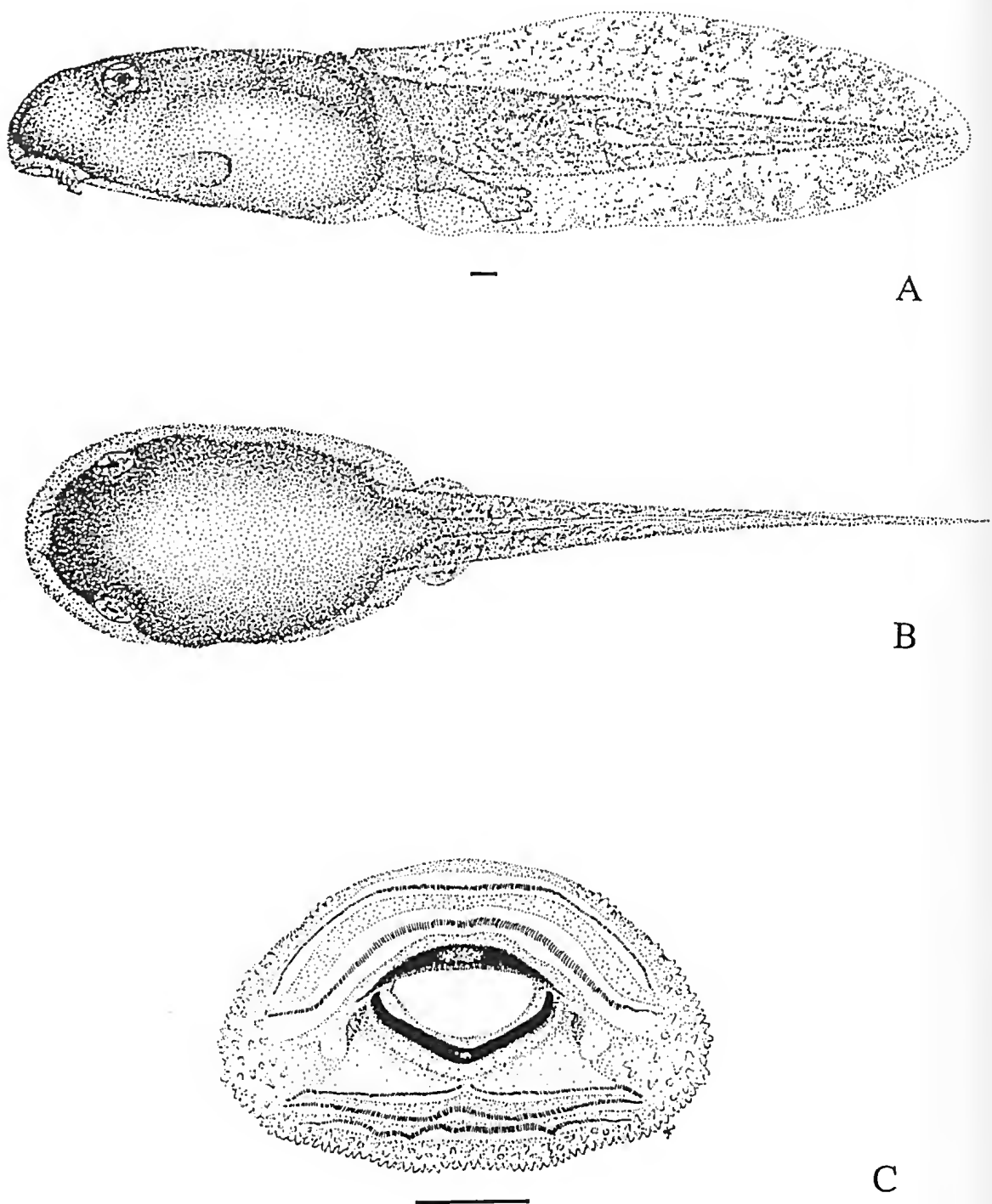
Fig. 2. Drawings from photographs of the tadpole of *Litoria spenceri*, Gosner stage 36 (NMV D66051) collected from the Big River (Mitta Mitta River) on 5 March 1992. Body length: 14.9 mm; total length: 35.7 mm; width of oral disc: 4.4 mm. A. Lateral view. B. Dorsal view. C. Oral disc. Solid bar represents 1 mm.

Two native fish species, the mountain galaxid (*Galaxias olidus*) and the river blackfish (*Gadopsis marmoratus*), and two exotic species, rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) were often observed in the vicinity of tadpoles. This suggests that tadpoles of *L. spenceri* have defence mechanisms against fish predation. However, the effects of introduced trout species on tadpole survival are not known.

Sympatric species

Tadpoles of *L. spenceri* were found in sympatry with *L. lesueuri* on the Big and Taponga rivers, with *L. phyllochroa* and *L. lesueuri* on the Wongungarra River, with *L. phyllochroa* on Bogong Creek, and *L. lesueuri* and *L. ewingii* complex tadpoles in an isolated streamside pool on the Black River. *Litoria citropa* has been found in adjacent river systems but is not known to occur with *L. spenceri*. Hero & Gillespie (1993) have provided information on distinguishing these riverine tadpoles in the field.

The tadpole of *L. phyllochroa* is the most easily confused with that of *L. spenceri*. Superficially *L. spenceri* tadpoles are slightly more dorsoventrally compressed, with eyes more dorsally oriented than *L. phyllochroa*. The uniform distribution of chromataphores on the flanks of *L. spenceri* tadpoles generally contrasts with that of *L. phyllochroa*, which usually has clusters of gold and black chromataphores on the flanks which produce striations or blotches. However, the most reliable diagnostic characteristic is the oral disc which is wider in *L. spenceri* than *L. phyllochroa* (body length/oral disc ratio <3.8 versus >3.8 respectively; Hero & Gillespie 1993).

ACKNOWLEDGEMENTS

REFERENCES

ANZECC, 1991. Australian and New Zealand Environmental Conservation Council. List of Endangered Vertebrate Fauna. (ANPWS: Canberra).

ALTIG, R., 1970. A key to the tadpoles of the continental United States and Canada. *Herpetologica* 26: 180–207.

BRAGG, A. N., 1957. Variations in colors and color patterns in tadpoles in Oklahoma. *Copeia* 1957: 36–39.

EHMANN, H., EHMANN, J. & EHMANN, N., 1993. The rediscovery of the endangered Spotted Tree Frog (*Litoria spenceri*) in New South Wales and some subsequent findings. *Herpetofauna* 22(2): 21–24.

GILLESPIE, G. R., 1992. Survey for the Spotted Tree Frog (*Litoria spenceri*) in Victoria, February–March 1992. *Victorian Naturalist* 109: 203–211.

GILLESPIE, G. R., 1993. Distribution and Abundance of the Spotted Tree Frog (*Litoria spenceri*) in Victoria. Unpublished report to the Australian National Parks and Wildlife Service, Endangered Species Unit, Canberra, 29 p.

GOSNER, K. L., 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16: 183–190.

HERO, J.-M., 1990a. The status of the Spotted Tree Frog (*Litoria spenceri*) in the Mount Murray Forest Block. Unpublished report to the Department of Conservation and Environment, Victoria.

HERO, J-M., 1990b. An illustrated key to the tadpoles occurring in the Central Amazon rainforest, Manaus, Amazonas, Brasil. *Amazoniana* 11: 201–262.

HERO, J.-M., 1991. A froggy forecast: the search for Victoria's rarest tree frog. *Wildlife Australia* Autumn 1991: 14–15.

HERO, J.-M. & GILLESPIE, G. R., 1993. The tadpole of *Litoria phyllochroa* (Anura, Hylidae). *Proceedings of the Royal Society of Victoria* 105(1): 31–38.

OSBORNE, W. S., GILLESPIE, G. R. & KUKOLIC, K., 1994. The Spotted Tree Frog *Litoria spenceri*: an addition to the amphibian fauna of the Australian Capital Territory. *Victorian Naturalist* 111(2): 60–64.

WATSON, G. F., LITTLEJOHN, M. J., HERO, J.-M. & ROBERTSON, P., 1991. *Conservation Status, Ecology and Management of the Spotted Tree Frog (*Litoria spenceri*)*. Arthur Rylah Institute for Environmental Research Technical Report Series No. 116, Department of Conservation and Environment, 40 p.

DISTRIBUTION OF THE ENDANGERED OTWAY STONEFLY
EUSTHENIA NOTHOFAGI ZWICK (PLECOPTERA:EUSTHENIIDAE)
IN THE OTWAY RANGES

T. Doeg & J. Reed

Flora and Fauna Branch, Department of Conservation and Natural Resources, 123 Brown Street,
Heidelberg, Victoria 3084

Doeg, T. & Reed, J., 1995:07:31. Distribution of the Endangered Otway stonefly *Eusthenia nothofagi* Zwick (Plecoptera:Eustheniidae) in the Otway Ranges. *Proceedings of the Royal Society of Victoria* 107 (1): 45–50. ISSN 0035-9211.

A survey for the Otway stonefly *Eusthenia nothofagi* Zwick (Plecoptera:Eustheniidae) was conducted throughout the Otway Ranges, south-west Victoria. Members of the genus were located at 19 out of 52 sites sampled, widely spread through the ranges. Sites where the genus was present were located primarily in streams draining cool temperate rainforest, and wet sclerophyll forest. The main in-stream habitats where nymphs were collected were under cobbles and wood, usually restricted to slower flowing areas along the edge of stream.

Late instar nymphs were collected at 11 sites and reared through to adults. This confirmed the presence of the species *Eusthenia nothofagi* at 9 sites widely distributed throughout the Otway Ranges. No adults of *Eusthenia venosa* were reared, and it is therefore assumed that all *Eusthenia* nymphs represent records for *Eusthenia nothofagi* and that the species is widely distributed in the Otway Ranges and would probably be located within virtually all the catchments in the region, including closed catchments, reference areas and special reserves.

In our opinion, the combination of sites in areas of secure land-use, and the application of local Public Land management, is likely to provide sufficient protection to ensure the survival and future evolutionary potential of the species.

THE STONEFLY family Eustheniidae (Insecta: Plecoptera) is considered to be of high scientific interest as it is believed to be the most archaic and least evolved of the stoneflies. Zwick (1979) quotes Tillyard (1921) as concluding that 'though existing to-day, they represent the original archetypic family of the Order, from which all other types must have been derived'. The distribution of the family and sub-families is also believed to be of considerable zoogeographic interest (Campbell 1981, cited in IUCN 1983).

Following a review of the family, Zwick (1979) erected the Otway stonefly, *Eusthenia nothofagi* Zwick, on the basis of differences in adult male genitalia from the other species in the genus, *E. venosa* (Tillyard). This decision was based on adult male specimens held in the Museum of Victoria (holotype from Beech Forest collected in January 1932). Adult females, from the same location and date, and from 1 km west of Apollo Bay (no date or collector) could not be positively assigned to either species as females 'seem to be similar in both species' (Zwick 1979, p. 37). However, without providing any definitive reason, Zwick stated that the two species (*E. venosa* and *E. nothofagi*) do not occur together. This has subsequently been taken to mean that *E. nothofagi* is restricted to the Otway Ranges, while *E. venosa*

is widespread throughout the rest of Victoria.

On the basis of the presence of only a single confirmed location, *E. nothofagi* was listed as Endangered, defined as 'taxa in danger of extinction and whose survival is unlikely if the causal factors continue operating' (IUCN 1983) by the International Union for Conservation of Nature and Natural Resources, and as Endangered by Department of Conservation and Natural Resources (CNR 1993). The species was listed under the *Flora and Fauna Guarantee Act* 1988 (SAC 1991) in May 1991 as presumed extinct on the basis that it had not been positively sighted for more than 40 years.

However, in April 1991, a male adult stonefly, subsequently identified as *E. nothofagi*, was collected by P. Lilywhite of the Museum of Victoria at Melba Gully State Park, near Lavers Hill (formal confirmation of the identification was made after the final *Flora and Fauna Guarantee Act* listing as presumed extinct). This was the first official record of the taxon since the original specimen from which the species description was made.

In 1993, the Australian Nature Conservation Agency (ANCA) funded a project to determine the true distribution of the species as a preliminary action to the preparation of a formal Recovery Plan. This paper presents the results of the survey.

METHODS

Fifty-two sites were selected from across the Otway Ranges region (Fig. 1), primarily within the forested areas, but extending outwards into the agricultural flats surrounding the ranges. Sampling trips were conducted in March, September, October and November 1993 and in December 1994. Over this period, all sites were visited at least once (some were revisited to collect live larvae for rearing). As a long-lived species, probably spending some years in the larval phase, it is unlikely that the timing of the surveys primarily over spring and summer would have influenced the observed distribution of the species.

At each site, a total of one person-hour was spent searching in the stream for *Eusthenia* nymphs. All habitat types within the stream (primarily wood debris and stones, in backwaters and the main channel) were included. Possible habitat elements at each site were lifted and examined by eye for nymphs (this was possible due to the large size of the larvae). The number of *Eusthenia* located and the habitat in which they were found was recorded. Although not strictly quantitative, this technique provided relative abundance figures which could be compared between sites. Additionally, a further 15–30 minutes were spent inspecting the surrounding vegetation and ground for possible adult eustheniid stoneflies.

Late instar nymphs of *Eusthenia* (identified by the presence of large wingpads) were collected from 11 sites and transported live to the laboratory in plastic bags half filled with water with a pure oxygen atmosphere. Bags were placed in a cooler and covered in ice. This technique was found to result in no mortality of the nymphs during transport.

Individual nymphs were placed in net-covered cages suspended in a flow-through of aquarium water maintained at 17°C. These were checked each day and emergent adults were collected, preserved and identified.

RESULTS

Distribution

Nymphs of the genus *Eusthenia* were recorded at 19 sites (Fig. 1). These were distributed over a wide area of the Otways, from the Johanna River (at Melba Gully State Park) and Chapple Creek (a tributary of the lower Gellibrand River) in the west, to the Erskine River at Erskine Falls in the east. Sites covered almost the entire range of altitudes found in the Otway Ranges. In the majority of cases, sites were located in forested areas (cool temperate rainforest, and wet sclerophyll forest), in State Forest or National Park. Two sites (the Ford and East Barham Rivers) were in areas where agricultural clearing was relatively extensive (although the specific sites were wide streams with abundant local riparian vegetation and little obvious impact of clearing) and one (the Aire River at the Redwoods) was located primarily in pine forests. The majority of sites in State Forest had been subjected to timber harvesting activities at various intensities in the past.

Sites where larvae were not located were in incised streams where agriculture was the prevalent land-use (and where suitable slow flowing areas or habitat were absent), where some other major disturbance was obvious (e.g. downstream of the West Barwon Reservoir) and coastal streams at low altitudes (again primarily in cleared land).

No adults were located in the field during the survey.

In-stream habitat

The main habitats within the stream containing larvae were the undersides of cobbles and wood, and usually restricted to slow flowing areas within, or along the side of the stream. These cobbles or wood were generally not embedded in any deposited silt in backwaters, although some had silt deposited on their surface. However, this in-stream habitat was not exclusive, as some nymphs were located in mid-stream where the current velocity was fast.

Relative abundance

Although the number of nymphs recorded during a single person-hour search cannot be regarded as a quantitative measure of abundance (expressed in numbers per metre square of stream bed), it does allow a comparison of the numbers collected between sites.

The sites where nymphs were most abundant were at Sabine Falls (Site 37 in Fig. 1: 22 individuals), in the Johanna River at Melba Gully (Site 9: 11), West Arkins Creek (Site 3: 7), Erskine River (Site 19: 5), Carlisle River (Site 47: 4), Cumberland River (Site 39: 4) and Parker River (Site 4: 4). At the remaining sites, fewer than 4 individuals were collected.

The sites at Sabine Falls and the West Arkins Creek were the two highest sites sampled during the survey (500 m ASL), and there was a significant linear correlation between altitude and the number of nymphs collected during the standard search time (Fig. 2: $r = 0.619$, $df = 13$, $p < 0.05$).
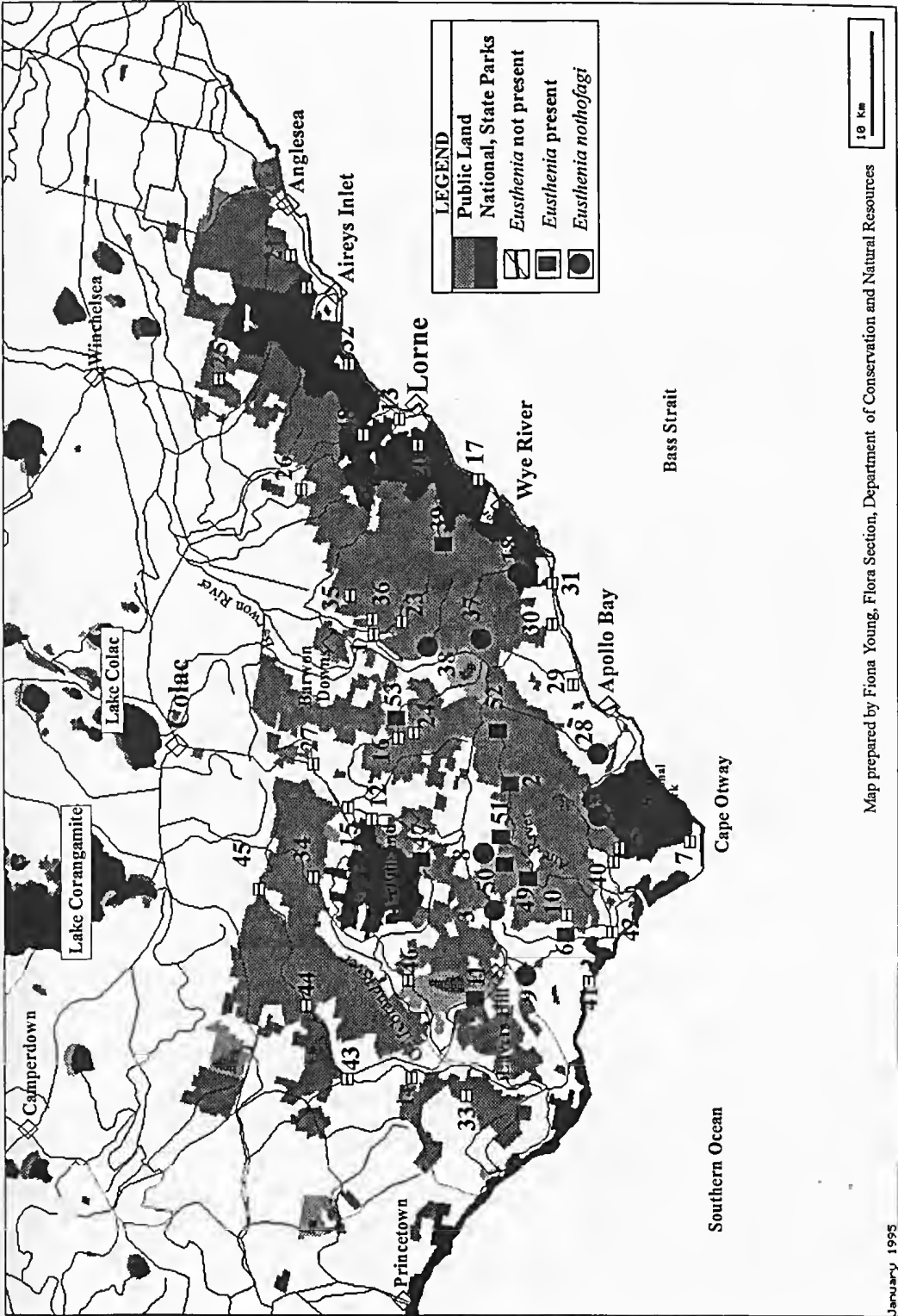
Fig. 1. Map of the Otway Ranges showing the location of sampling sites. Numbers refer to site numbers used in the survey.

Even if the Sabine Falls site (the possible outlier site in Fig. 2) is excluded from the correlation, there is still a significant positive relationship between altitude and abundance ($r = 0.565$, $df = 12$, $p < 0.05$). It would therefore appear that larger populations of the stonefly are found in higher altitude steams, although populations occur throughout the range of altitudes within the Otways (the lowest altitude where *Eusthenia* nymphs were recorded was only 40 m ASL).

Rearing trials

Twenty of the nymphs, from 11 sites, were successfully reared through to the adult stage (Table 1). Adult males were reared from 9 sites. In all cases, these were positively identified as *Eusthenia nothofagi*. Adult females were reared from 6 sites and could not be positively identified.

DISCUSSION

It is clear from the results of this survey that the Otway stonefly is spread throughout the forested areas of the Otway Ranges (at least from Melba Gully in the west, to Lorne in the east, a distance of some 50-60 km).

While there was a trend towards larger populations at higher altitudes, there is no apparent distinct trend in local conditions that would allow an estimate of likely population sizes to be made for any unsampled site. The size of streams ranged from small (<1 m wide at Sabine Falls and the

Site	Males	Females
Aire River (2)		1
West Arkins Creek (3)	1	1
Johanna River (9)	2	1
Young Creek (8)	1	
Grey River (18)	1	
Erskine River (19)	2	3
East Barham River (28)	1	
Trib. of Smyths Creek (37)	1	2
Parker River (4)	1	
Barwon River (38)	1	
Cumberland River (39)		1

Table 1. Number of adults that successfully emerged in the laboratory (site number from Fig. 1 in parentheses).

Parker River) through to relatively large (5–10 m wide at Erskine Falls and the Cumberland River). Substrata also varied somewhat between these sites, from predominantly cobbles and boulders (Erskine Falls), through cobbles and bedrock (Sabine Falls), cobbles and sand (West Arkins Creek) to mainly smaller pebbles and sand (Carlisle River) and even to a substratum composed almost entirely of compacted clay (Parker River at Maits Rest).

While the majority of these sites were in areas where the riparian vegetation formed an almost totally closed canopy, which created a dark humid streamside environment (Sabine Falls, West Arkins Creek, Parker River, Johanna River), other sites were located in more open sclerophyll forest
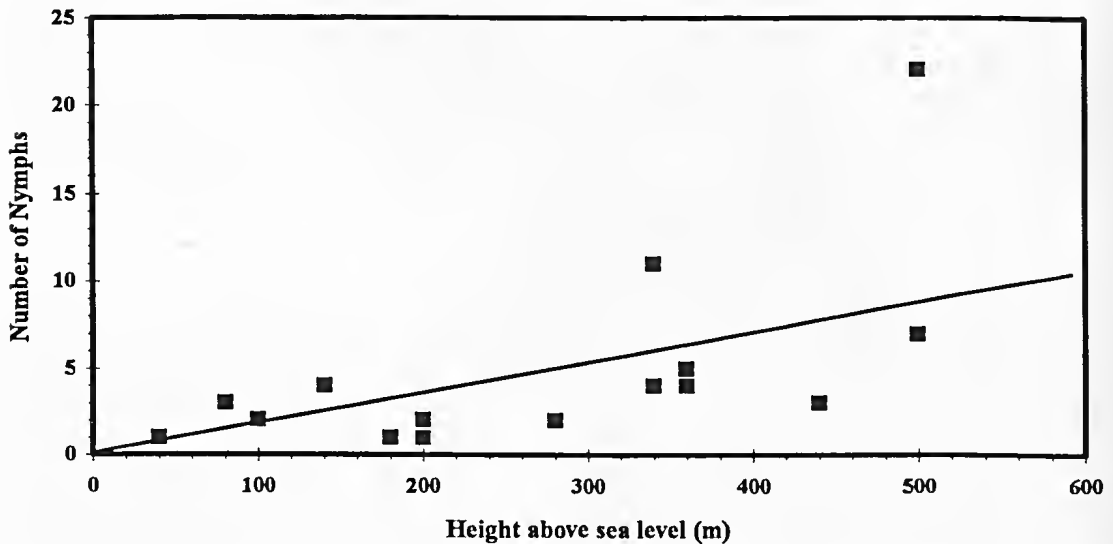
Fig. 2. Number of nymphs collected per hour plotted against the altitude of the site.

(Cumberland River, Erskine River) and in one ease where the stream surfaee was open to the full sun (Carlisle River).

This lack of eonsisteney between sites in their general environmental features is partly explained by the observation that nymphs were often (but not exclusively) found in slower flowing areas along the side of the stream. The presence of these baekwaters is probably independent of many of the physical attributes of the stream, so that suitable mierohabitat areas ean be loeated in streams with a wide variety of maerohabitats.

Based on this survey, it is impossible to prediet aeeurately the general eonditions within a stream that would lead to high populations of the species, or the speeifie conditions that lead to higher populations at higher altitudes. However, the eonditions where the speeies was loeated (ineluding those that produeed higher densities) are common and widespread throughout the Otways, suggesting that the speeies is similarly distributed.

In terms of land-use, many suitable sites within the Otway Ranges are loeated in National Parks or areas seeure from major disturbanee (e.g. elosed water eatchments). In the main, areas in State Forest open to timber harvesting are governed by loeal forestry preeriptions designed to proteet aquatie resourees (DCE 1991).

The original belief that the Otway stonefly was endangered is a product of the laek of eomprehensive surveys of the area and poor taxonomie knowledge. Poor survey eoverage or taxonomic knowledge are eommon for freshwater maeroinvertebrates and there are many examples where taxonomy is based on adult features, when the most often eolleeted forms are larvae or nymphs. While sueh problems are slowly being addressed through inereased survey aetivity (such as this study) and improved taxonomie proeedures, it is likely that further work will reveal that some taxa eonsidered rare are, in faet, eommon. On the other hand, improved survey and distributional knowledge will undoubtedly inerease the number of taxa that will be shown to be rare or threatened (Buteher & Doeg 1995). Of the potentially thousands of aquatie maeroinvertebrate speeies present in Vietoria, only 23 are listed as rare, vulnerable or threatened in Vietoria, and only 14 speeies are listed under the *Flora and Fauna Guarantee Act 1988*.

It is not possible to determine whieh of the formal eonservation categories used to describe species (1UCN 1983; CNR 1993) would apply to the Otway stonefly. While demonstrably not Extinet or Endangered (as eurrently elassified), it eannot be placed within the Vulnerable, Rare or Insuffieiently Known categories (as these require demonstrable deeline). Of more value would be a eategory like Restricted (Jaekson et al. 1993), indieating a taxon that is not in apparent danger but occurs in a relatively small area.

Despite not being in immediate apparent danger, the Otway stonefly should still be seen an important speeies, being a living example of one of the oldest known insect orders. It can also be seen as a loeally signifieant speeies, endemie to a eomparatively small area of Vietoria. The presenee of other invertebrate speeies restricted to the Otway Ranges (including the Blaek Otway Snail *Victaphanta compacta*, the erayfish *Engaeus fultoni*, the gripopterygid stonefly *Illiesoperla austrosimplex* and the caddisfly *Taskiria otwayensis*) would seem to suggest that a number of yet undiseovered or undeseribed speeies may well be endemic to the area. So, while loeally eommon, *Eusthenia nothofagi* may fill the requirements for the role of a 'flagship taxon', one that ean be seen as a representative for all the unique taxa present at a locale and ean be utilised to highlight and raise awareness of freshwater and invertebrate issues (Yen & Buteher 1994). As sueh, it has a eonservation signifieanee that is not due to rarity or some formal threatened status. And with this in mind, the Otway stonefly is still worthy of eonscious proteetion measures.

CONCLUSIONS

The Otway stonefly *Eusthenia nothofagi* Zwiek is widespread throughout forested areas within the Otway Ranges. Although probably most eommon in small upland tributaries, the speeies ean be loeated in a wide variety of stream types, in terms of stream size, bed composition and riparian eondition.

ACKNOWLEDGEMENTS

REFERENCES

BUTCHER, R. & DOEG, T., 1995. Conservation of freshwater invertebrates. *Victorian Naturalist* 112: 15–19.

CAMPBELL, I. C., 1981. Biogeography of some rheo-
    philous aquatic insects in the Australasian region.
    Aquatic Insects 3: 33–43.
CNR, 1993. *Threatened Fauna in Victoria.* Depart-
    ment of Conservation and Natural Resources,
    Melbourne.
DCE, 1991. *Proposed Forest Management Plan: Otway
    Forest Management Area.* Department of Con-
    servation and Environment, Melbourne.
IUCN, 1983. *The IUCN Invertebrate Red Data Book.*
    International Union for Conservation of Nature
    and Natural Resources, Switzerland.
JACKSON, P. D., KOEHN, J. D. & WAGER, R., 1993.
    Australia's threatened fishes 1992 listing—Aus-
    tralian Society for Fish Biology. In *Sustainable
    Fisheries through Sustaining Fish Habitat*, D. A.
    Hancock, ed., Australian Government Printing
    Service, Canberra.

SAC, 1991. Scientific Advisory Committee, Flora and
    Fauna Guarantee: Final recomendation on a
    Nomination for Listing: *Eusthenia nothofagi.*
    Department of Conservation and Environment,
    Victoria.
TILLYARD, R. J., 1921. Revision of the family Eust-
    heniidae (Order Perlaria) with descriptions of new
    genera and species. *Proceedings of the Linnaean
    Society of New South Wales* 46: 221–236.
YEN, A. & BUTCHER, R., 1994. *An Overview of the
    Conservation Status of Non-Marine Invertebrates
    in Australia.* Endangered Species Unit and Aus-
    tralian Nature Conservation Agency, Canberra.
ZWICK, P., 1979. Revision of the stonefly family Eust-
    heniidae (Plecoptera), with emphasis on the
    fauna of the Australian region. *Aquatic Insects*
    1: 17–50.

THE LATE PALAEOZOIC BRACHIOPOD GENUS *YAKOVLEVIA* FREDERICKS, 1925 AND THE *YAKOVLEVIA TRANSVERSA* ZONE, NORTHERN YUKON TERRITORY, CANADA

G. R. SHI

School of Aquatic Science and Natural Resources Management, Deakin University, Rusden Campus, 662 Blackburn Road, Clayton, Victoria 3168, Australia

SHI, G. R., 1995:07:31. The Late Palaeozoic brachiopod genus *Yakovlevia* Fredericks, 1925 and the *Yakovlevia transversa* Zone, northern Yukon Territory, Canada. *Proceedings of the Royal Society of Victoria* 107 (1): 51–71. ISSN 0035-9211.

The familial and superfamilial position, relationship with *Muirwoodia* Likharev, species composition, and stratigraphical and palaeogeographical distribution of *Yakovlevia* Fredericks are reviewed. *Muirwoodia* is considered to be a junior subjective synonym of *Yakovlevia*, which is placed in the Yakovleviidae Waterhouse within the Linoproductacea Stehli. Forty-five described (and/or illustrated) species ranging from the Middle Carboniferous to the mid-Permian (Wordian/Kazanian) from the Arctic, northeast China, Russian Far East, Japan, western North America, southwest United States, and Mexico are assigned to *Yakovlevia*. The palaeogeographical implications of the occurrences of the genus in northeast China, Japan, and United States–Central America is discussed. The *Yakovlevia transversa* Zone, most likely of Early Sakmarian (Tastubian) age, here established is based on material from the Jungle Creek Formation, northern Yukon Territory, Canada, and is correlated with several other faunas in the Arctic and western North America. *Yakovlevia transversa* (Cooper) is also described based on the Canadian material.

THE LATE PALAEOZOIC brachiopod productid genus *Yakovlevia* Fredericks (1925) is among the more characteristic brachiopod genera that distinguish the Late Palaeozoic Boreal Realm from the Tethyan and Gondwanan Realms to the south (Ustritskiy 1961; Shi & Waterhouse 1991). Biostratigraphically and palaeobiogeographically the genus is of particular interest because of its relatively short stratigraphical range, distinctive morphological characteristics, and restricted occurrences to the Northern Hemisphere [its occurrence in Chile recorded by Minato & Tazawa (1977) as *Muirwoodia* sp. is herein regarded as belonging to *Duartea* Mendes (1959), see discussion below]. The *Yakovlevia transversa* Zone recorded in this paper is traceable at many localities in the Arctic region and thus appears to represent a distinct time horizon of the Early Permian for the Boreal Realm.

Although *Yakovlevia* has been described since 1925, and the genus is morphologically distinctive, its systematic position is still a matter of debate. So far, it has been assigned to six different families: Productidae Gray, Paucispiniferidae Muir-Wood & Cooper, Retariidae Muir-Wood & Cooper, Anidanthidae Waterhouse, Linoproductidae Stehli, and Yakovleviidae Waterhouse. In addition, the relationship of *Yakovlevia* with *Muirwoodia* Likharev (1947) is still subjected to various opinions despite the earlier definitive study by Kotlyar (1961) who clearly showed that the two were not significantly different.

From 1988 to 1991, the author (Shi 1991) studied a large collection of Lower Permian brachiopods and molluscs from northern Yukon Territory, western Canada, among which there were well preserved specimens of *Yakovlevia transversa* (Cooper 1957) (see description later in the paper). The bulk of my thesis has been submitted to the Geological Survey of Canada for publication. The present paper provides a review of *Yakovlevia* based on the Canadian material, including discussions on its systematic position, its relationship to *Muirwoodia* and other related genera, and its stratigraphical and palaeogeographical distributions. Additionally, the paper also establishes *Yakovlevia transversa* Zone of the Sakmarian age based on material from the northern Yukon Territory of Canada, and attempts to correlate this zone with coeval faunas from North America and the Arctic. The species *Y. transversa* Cooper is also described and illustrated based on the Canadian collections.

The fossils described in this paper are registered by the prefix GSC and housed in the type collections of the Geological Survey of Canada, Ottawa. Two sets of locality numbers are used herein, one prefixed with GSC loc. with a five-figure serial number, representing fossil collections made by the officers of the Geological Survey of Canada, Dr E. W. Bamber in this case, and the other prefixed with JBW loc. with a two-figure serial number, representing collections made by Professor J. B. Waterhouse and colleagues during

expeditions to the study area between 1968 and 1972. Both field locality numbers are now registered with the Geological Survey of Canada, and the locality details have been provided by Waterhouse & Waddington (1982, Appendices 2 and 4).

RELATIONSHIP OF *YAKOVLEVIA* WITH *MUIRWOODIA*

Yakovlevia was proposed first as a subgenus of *Chonetes* Fischer de Waldheim by Fredericks (1925, p. 7) with the following description: 'Shell con-cavo-convex, productid-like, with area (interarea) in ventral valve. Ventral interior probably with development of apical plates and usually filled by secondary shell substance; anterior end of the apical plates extend forwards as well-developed ridges to enclose strongly depressed muscle field. Presence of a (ventral) median septum is not known.' The type species, *Y. kaluzinensis* Fredericks (1925), is represented only by ventral internal moulds, in which a high, about 3 mm across, transverse band is well shown along the hinge line (Fredericks 1925, pl. 2, figs 64–66). In establishing this sub-genus Fredericks noted the strong similarity of *Y. kaluzinensis* to productid shells, especially *Productus mammatus* Keyserling (1846).

Fredericks' diagnosis of *Yakovlevia*, particularly the presence of an 'interarea' with 'apical plates', was accepted by Likharev (1947), who subsequently proposed *Muirwoodia* for *Productus mammatus* Keyserling, chiefly on the basis that it has a thick-ened marginal area instead of an interarea with a median delthyrium supposedly characteristic of *Yakovlevia*. In their study of Productida Gray, Muir-Wood & Cooper (1960) also recognised *Muir-woodia* on similar accounts, but their conclusion was primarily based on observations on material from the Glass Mountains, West Texas, which they then regarded as *Muirwoodia* spp., but it should be noted that these Texas *Muirwoodia* spp. are now all placed in *Yakovlevia* by Cooper & Grant (1975) and the entire genus treated as a junior synonym of *Yakovlevia*. Other authors have also recognised *Muirwoodia*, wittingly or unwittingly (e.g. Dunbar 1955; Kashirtsev 1959; Gobbett 1964; Likharev & Kotlyar 1978; Kalashnikov 1980; Abramov & Grigor'yeva 1983; Duan & Li in Ding et al. 1985; Liu & Waterhouse 1985; Nakamura et al. 1987; Lazarev 1990).

Kotlyar (1961), on the other hand, critically examined the alleged presence of an 'interarea' and a 'delthyrium' in *Yakovlevia* based on more material and concluded that the so-called interarea was in reality 'none more than a thickened hinge margin which B. K. Likharev called "a marginal

area".' Kotlyar subsequently treated *Muirwoodia* as a junior subjective synonym of *Yakovlevia*. Similarly, Sarycheva et al. (1960), Likharev (1960, p. 484), Mironova (1964, 1967), Barchatova (1970), Stehli & Grant (1971), Ustritskiy (1971), Zavodovskiy & Stepanov (1971), Ifanova (1972), and Cooper & Grant (1975) have also considered the two to be synonymous. Grant (in Brabb & Grant 1971) effectively suppressed *Muirwoodia* by placing its type species, *Productus mammatus*, in *Yakovlevia*. Cooper & Grant (1975) described the thickened hinge margin as a ginglymus (Fig. 1A), which they showed among their excellently pre-served *Yakovlevia* from West Texas to be highly variable, suggesting that its formation is probably not genetically controlled but more probably an ecologically motivated feature. The ginglymus is not observed among the Canadian material as most of the specimens studied are either external or internal moulds, or separate valves.

In addition to the ginglymus, the hinge area of the ventral valve of *Yakovlevia* is usually marked by a well-demarcated transverse band just below or anterior to the gylingmus (see Fig. 1). Unlike the gylingmus which never reaches the cardinal extremities (Fig. 1A), the transverse band extends for the entire width of the hinge margin and, in some specimens, swings across the inner ears into lateral margins as low, flattened ridges that are often marked by striae (Figs 1B and 1C). On separate internal moulds of *Yakovlevia* from Yukon Territory, the transverse band is well pre-served in many specimens of ventral valves and marked by small, irregularly spaced tubercles (pits on internal moulds) (Fig. 1B). An identical transverse band along the hinge area of dorsal valves is also observed in the Canadian material and marked by tubercles (dimples on internal moulds) corresponding to pits on the ventral valves (Fig. 1C).

The function of the gylingmus, the transverse band, and the embedded pits and tubercles in *Yakovlevia* is not clear, but Cooper & Grant (1975) suggested that they may be related to helping with the articulation of these transverse shells.

The alleged presence of apical plates and a delthyrium in the ventral interior of *Yakovlevia* is clearly a misinterpretation, judged from obser-vations on the Canadian material as well as examination of the illustrations of *Yakovlevia* from Texas by Cooper & Grant (1975). One of the most conspicuous features that characterise *Yakovlevia* is its large, broadly heart-shaped muscle field on the posterior floor of the ventral interior (Figs 1B and 1C). The diductor scars are large, flabellate and deeply striate, separated anteriorly by a

thick, narrow platform whieh deereases in height posteriorly. The adduetor scars are located between but posterior to the diduetor scars and posteriorly separated from the latter by a layer of smooth callus that eovers mueh of the posterior part of the diduetors sears (Fig. 1A). The whole musele field is posteriorly loeated, deeply depressed, and encireled by strongly developed shell thickening, which in many specimens is strongly elevated and extends posteriorly right into the beak, therefore making a false impression of a delthyrium and apieal plates under the beak and the ginglymus (Figs 1A and 1B).

Apart from the misinterpretation of the thickened hinge margin (and ginglymus) and the posterior extension of the deeply depressed ventral muscle field, other internal struetures of both *Yakovlevia* and *Muirwoodia* have been considered to be essentially the same by many authors (Muir-Wood & Cooper 1960; Kotlyar 1961; Abramov & Grigor'yeva 1983). Thus, in view of the above observations and interpretation I suggest we follow Kotlyar (1961) and Cooper & Grant's (1975) conelusion that *Yakovlevia* and *Muirwoodia* are synonyms and the latter be suppressed as a eonsequenee.
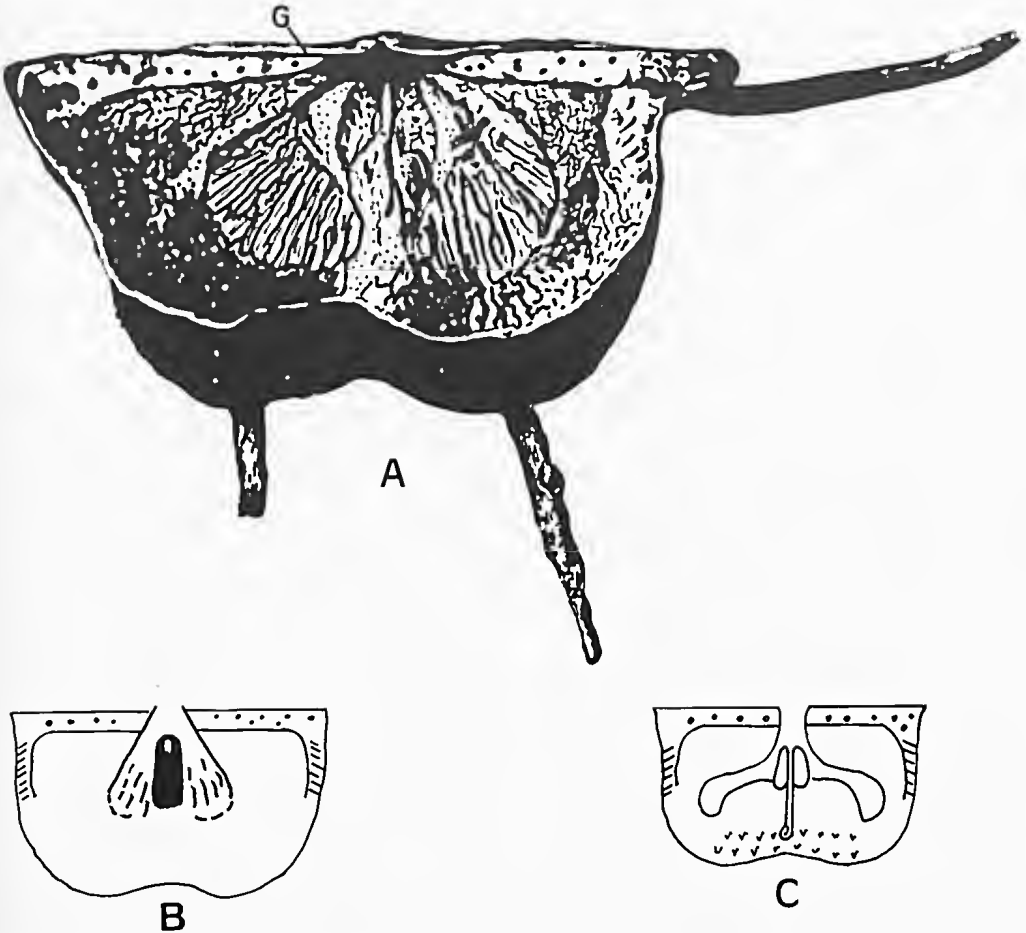
Fig. 1. A–C, Diagrams showing internal morphological characteristics of *Yakovlevia*. A, ventral interior of *Yakovlevia hessorum* Cooper & Grant (1975), redrawn from their pl. 473, fig. 1 to show the ginglymus (G), the reetangular transverse band below the ginglymus, and the ventral musele field, ×2.1; B, C, *Yakovlevia transversa* (Cooper) from northern Yukon Territory, Canada, showing ventral and dorsal interiors, respectively. (Fig. 1B drawn from a ventral internal mould and Fig. 1C from a latex east of a dorsal internal mould, both ×1.2 approximately.)

FAMILIAL POSITION OF *YAKOVLEVIA*

There have been varied opinions among brachiopod workers over the familial position of *Yakovlevia* (and *Muirwoodia*). Fredericks (1925) originally compared *Yakovlevia* with *Productus* Sowerby and placed the former in the Chonetinae Bronn. Likharev (1947) proposed *Muirwoodia* as a subgenus of *Productus* but did not comment specifically on its familial/subfamilial position although the Productidae Gray may have been implied by him. This classification was also used by Kashirtsev (1959) and Sarycheva et al. (1960). More recent studies on *Yakovlevia* (and *Muirwoodia*) have demonstrated a broader range of potential familial positions for *Yakovlevia*. Muir-Wood & Cooper (1960) assigned *Yakovlevia* (and *Muirwoodia*) to their newly proposed subfamily Paucispiniferinae within the Linoproductidae Stehli. This grouping was based on the fact that both *Yakovlevia* (and *Muirwoodia*) and *Paucispinifera* are characterised by few (four or more) halteroid spines and a sessile, dorsally recurved, trilobate cardinal process. This classification was subsequently adopted by Muir-Wood (1965) and Barchatova (1970). However, Waterhouse & Piyasin (1970, p. 92) rejected this scheme, arguing that (1) the Paucispiniferinae 'is clearly Marginiferid', and (2) 'Genera associated with *Paucispinifera* by these authors (Muir-Wood & Cooper) such as *Yakovlevia* and *Muirwoodia* are not Marginiferid', but rather probably 'belong with the Linoproductidae'. This argument was later reinforced and formalised by Waterhouse (1975) by proposing the new subfamily Yakovleviinae within the Linoproductidae, in which he included three genera: *Yakovlevia*, *Muirwoodia* and *Duartea* Mendes (1959). Waterhouse (1978) uplifted the Yakovleviinae to the family rank within the superfamily Linoproductacea. Independently, Cooper & Grant (1975) also separated *Yakovlevia* from the Paucispiniferidae and placed it in the Linoproductidae. Kalashnikov (1980), on the other hand, while recognising *Muirwoodia* assigned this genus to the Retariidae Muir-Wood & Cooper on the grounds that the dorsal interior of *Muirwoodia pseudoartiensis* (Stuckenberg) he described shows cardinal and lateral ridges and a diaphragm, resembling the dorsal interior of *Retaria* Muir-Wood & Cooper and allies. Kalashnikov's proposition was however not accepted by Abramov & Grigor'yeva (1983), who pointed out that the cardinal and lateral ridges and the diaphragm were not persistent features for all *Muirwoodia* species and certainly not present in *M. mammata* (Keyserling), the type species of the genus. These authors instead recognised the Yakovleviidae.

Another opinion regarding the familial assignment of *Yakovlevia* was expressed by Kalashnikov (in Mcyen 1983), who linked the genus to the Anidanthidae Waterhouse, but no explanation was given. More recently, Lazarev (1990) also recognised the family Yakovleviidae but he placed it in the superfamily Productacea, arguing that (1) the early representative of the Yakovleviidae, *Sajakella* Nasikanova (in Grigor'yeva & Nasikanova 1968), has coarser costellae that resemble those of the Inflatiidae Sarycheva, and (2) that there exists 'striking similarity' in dorsal internal structures between *Yakovlevia* and representatives of *Horridonia* Chao, although no specific comparisons were given.

In this paper, I also recognise the family Yakovleviidae but disagree with Lazarev on his classification of this family with the Productacea on three main grounds. Firstly, although *Sajakella formosa* Nasikanova (in Grigor'yeva & Nasikanova 1968), type species of *Sajakella*, has costellate appearance that indeed suggests similarity to *Inflatia* Muir-Wood & Cooper and allies, but *Inflatia* and related genera lack the four or more halteroid spines that characterise *Sajakella* and other yakovleviid genera and have usually much coarser costellae, a strongly convex visceral disc, a roundedly geniculated trail, and a prominent reticulation pattern on the visceral disc. To the contrary, I would argue that the fine capillate to costellate exterior of the Yakovleviidae alone clearly relate this group to the linoproductids. Secondly, although the transverse outline, flattened visceral disc, and the paucity of long, erect halteroid spines of *Yakovlevia* and allies appear to suggest some degree of resemblance to *Paucispinifera*, as noted initially by Muir-Wood & Cooper (1960), but the latter has strong marginal ridges and a cardinal process allied to that of *Marginifera* Waagen and *Kozlowskia* Fredericks, all with a distinct zygidium. In addition, *Yakovlevia* and *Paucispinifera* differ significantly in the distribution pattern of their halteroid spines; the former always has four basic halteroid spines: one on each ear and one on the trail on each side of the sulcus just anterior to the venter, as opposed to *Paucispinifera* which always has six large halteroid spines: one on each ear, one on each umbonal slope, and one on each side of the sulcus, as well as a row of additional smaller spines up the furrow demarcating ears (Muir-Wood & Cooper 1960, p. 320). Thirdly, Lazarev's observation that *Yakovlevia* has 'striking similarity' in dorsal internal structures to those of *Horridonia* is probably inadequate because the former usually has well-differentiated anterior and posterior adductor scars at maturity and a much lower

cardinal process with separated lobes typical of the linoproductids (see Muir-Wood & Cooper 1960: pl. 120, fig. 7; Cooper & Grant 1975: pl. 471, fig. 22) compared with the dorsal interior of *Horridonia*, which is characterised by non- or ill-differentiated adductor scars and a high cardinal process usually supported by a shaft (see Muir-Wood & Cooper 1960: pl. 108, fig. 8).

STRATIGRAPHICAL AND PALAEOGEOGRAPHICAL DISTRIBUTION OF *YAKOVLEVIA*

Forty-seven species have been recorded previously under the names of *Yakovlevia* and *Muirwoodia*, most of them having been described and illustrated. Of these, 45 are recognised in this paper in view of the definition of *Yakovlevia* adopted herein (Table 1, Fig. 2). The other two recorded forms that are excluded from this list are *Muirwoodia*? *aurita* Volgin (1960) from the Middle Carboniferous Uchbulak Horizon of Fergana and *Muirwoodia* sp. (Minato & Tazawa 1977) from the Lower or Middle Permian unnamed strata in southern Chile. The first species probably belongs to *Protanidanthus* Liao (1979) for it has a strongly transverse and fusiform outline, a strong but rounded geniculation of the ventral valve, poorly demarcated ears, and coarse costellae. The Chilean species recorded by Minato & Tazawa is represented by three poorly preserved specimens; they are probably either a *Duartea* sp. or an *Anidanthus* sp. Very little was known about the ventral valve except for a large halteroid spine extruding from one ear, suggesting *Yakovlevia* or *Duartea*, but the dorsal valve was said to be covered with undulated rugae in addition to costellae, resembling the dorsal ornament of *Anidanthus* Whitehouse, or allies.

It is clear from Table 1 and Fig. 2 that *Yakovlevia* has both a restricted stratigraphical and geographical distribution. The genus first appeared in the Middle Carboniferous in the Urals and Russian Platform, probably evolved from *Sajakella* through *Productus martianovi* Lapina (1957), a species assigned tentatively to *Sajakella* by Nasikanova (in Grigor'yeva & Nasikanova 1968) but transferred to '*Muirwoodia*' by Kalashnikov (1980), due to its 'transitional' characteristics, especially in external
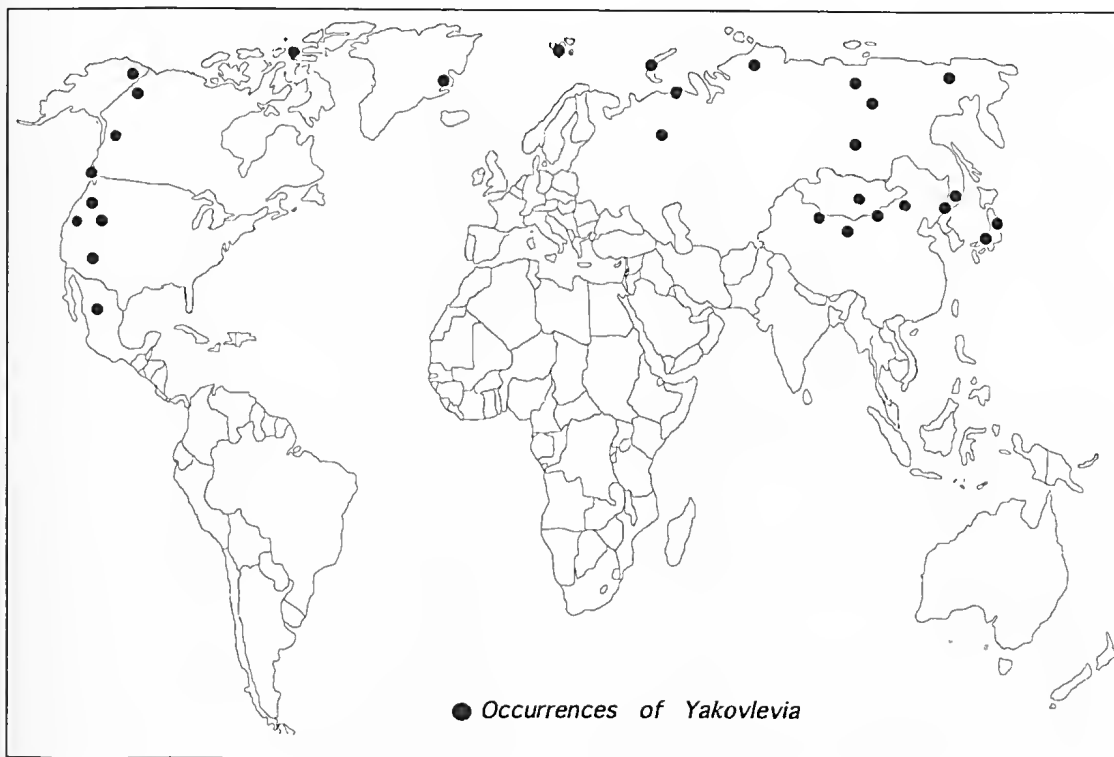
Fig. 2. Global occurrences of *Yakovlevia* species recognised in this paper.

Species	Geographic distribution	Age range	Key references
Yakovlevia mammata (Keyserling 1846)	The Urals, Novaya Zemlya, NE Siberia, Taimyr Peninsula, Spitsbergen, Mongolia, NE China, Canada, Alaska, Spitsbergen; Greenland	?Asselian to Kungurian	Chernyshev 1902; Kashirtsev 1959; Harker & Thorsteinsson 1960; Zavodovskiy & Stepanov 1971; Brabb & Grant 1971; Nakamura et al. 1992
Yakovlevia multistriata (Meek 1860)	Phosphoria and Park City Formations, Great Basin, U.S.A.	Wordian (?Kazanian)	Yochelson 1968
Yakovlevia weyprechti (partim.) (Toula 1873)	Kapp Starostin Formation and equivalents in Spitsbergen and Greenland	Kungurian-Ufimian	Toula 1873; Wiman 1914; Dunbar 1955; Nakamura et al. 1992
Yakovlevia impressa (Toula 1875)	Kapp Starostin Formation and equivalents in Spitsbergen and Greenland	Kungurian-Ufimian	Toula 1875; Wiman 1914; Dunbar 1955; Nakamura et al. 1992
Yakovlevia artiensis (Chernyshev 1889)	The Urals and Russian Platform	U. Carboniferous to Artinskian	Chernyshev 1889; Kalashnikov 1980
Yakovlevia pseudo-artiensis (Stuckenberg 1905)	The Urals and Russian Platform	U. Carboniferous to Artinskian	Stuckenberg 1905; Kalashnikov 1980
Yakovlevia geniculata (Girty 1910)	Park City Formation, Idaho, U.S.A.	Wordian (?Kazanian)	Girty 1910
Yakovlevia duplex (Wiman 1914)	Kapp Starostin Formation and equivalents in Spitsbergen and Greenland	Kungurian-Ufimian	Wiman 1914; Dunbar 1955; Nakamura et al. 1992
Yakovlevia kaluzinensis Fredericks 1925	Chandlaz Suite, Sikhote Alin, Russia	Kungurian-Ufimian	Fredericks 1925; Likharev & Kotlyar 1978
Yakovlevia mammati-formis (Fredericks 1926)	The Urals and NE Siberia, Mongolia and north China	Sakmarian-Artinskian	Fredericks 1926; Ustritskiy 1971
Yakovlevia svalbardensis Frebold 1937	Spitsbergen	Kungurian-Ufimian	Frebold 1937
Yakovlevia deminutivus (Cloud 1940)	Mexico	Early Permian	Cloud 1944
Yakovlevia sp.	Monos Formation, Mexico	Wordian (?Kazanian)	Cooper in Cooper et al. 1953
Yakovlevia greenlandica (Dunbar 1955)	Kapp Starostin Formation or equivalents, Spitsbergen and Greenland	Kungurian to Ufimian	Dunbar 1955; Gobbett 1964; Nakamura et al. 1992
Yakovlevia transversa (Cooper 1957)	Coyote Butte Formation, central Oregon; Jungle Creek Fm., Yukon Territory; Vancouver Island	Sakmarian to ?Kungurian	Cooper 1957; this paper
Yakovlevia californica (Coogan 1960)	Nosoni Formation, northern California	?Kungurian	Coogan 1960
Yakovlevia timanica Barchatova 1970	Timan Range, Russia	Kungurian	Barchatova 1970
Yakovlevia paraimpressa Barchatova 1970	Timan Range, Russia	Kungurian	Barchatova 1970
Yakovlevia anterospinosa Cooper and Grant 1975	Road Canyon Fm., Texas	Roadian (Kungurian-Ufimian)	Cooper & Grant 1975
Yakovlevia sulcata Cooper and Grant 1975	Road Canyon Fm., Texas	Roadian (Kungurian-Ufimian)	Cooper & Grant 1975
Yakovlevia costellata Cooper and Grant 1975	Cherry Canyon Fm., Texas	Wordian (?Kazanian)	Cooper & Grant 1975

Table 1.   Stratigraphic and geographic distribution of *Yakovlevia* (= *Muirwoodia*) species.

Species	Geographic distribution	Age range	Key references
Yakovlevia immatura Cooper and Grant 1975	Road Canyon Fm., Texas	Roadian (Kungurian-Ufimian)	Cooper & Grant 1975
Yakovlevia hessorum Cooper and Grant 1975	Word Fm., Texas	Wordian (?Kazanian)	Cooper & Grant 1975
Yakovlevia indentata Cooper and Grant 1975	Word Fm., Texas	Wordian (?Kazanian)	Cooper & Grant 1975
Yakovlevia intermedia Cooper and Grant 1975	Word Fm., Texas	Wordian (?Kazanian)	Cooper & Grant 1975
Yakovlevia mucronata (Lee and Gu 1976)	Zhesi Fm., Inner Mongolia, NE China	Artinskian-Kungurian	Li & Gu 1976
Yakovlevia baerginensis Lee and Gu 1976	Zhesi Fm., Inner Mongolia, NE China	Artinskian-Kungurian	Li & Gu 1976
Yakovlevia unsinuata Lee and Gu 1976	Zhesi Fm., Inner Mongolia, NE China	Artinskian-Kungurian	Li & Gu 1976
Yakovlevia ambiguia Lee and Gu 1976	Zhesi Fm., Inner Mongolia, NE China	Artinskian-Kungurian	Li & Gu 1976
Yakovlevia penusa Lee and Gu 1976	Zhesi Fm., Inner Mongolia, NE China	Artinskian-Kungurian	Li & Gu 1976
Yakovlevia baiyinensis Lee and Gu 1976	Zhesi Fm., Inner Mongolia, NE China	Artinskian-Kungurian	Li & Gu 1976
Yakovlevia paramammata Lee and Gu 1980	Sijiashan Fm., Helongjiang Prov., NE China	Artinskian-Kungurian	Li & Gu 1980
Yakovlevia complanata Lee and Gu 1980	Wujiatong Fm., Helongjiang Prov., NE China	Artinskian-Kungurian	Li & Gu 1980
Yakovlevia paragreenlandica Lee and Gu 1980	Dashisai Fm., Helongjiang Prov., NE China	Artinskian-Kungurian	Li et al. 1980
Yakovlevia taxiensis Lee and Gu 1980	Tumenling Fm., Helongjiang Prov., NE China	Artinskian-Kungurian	Li et al. 1980
Yakovlevia dimorpha Lee and Gu 1980	Dashisai, Helongjiang Prov., NE China	Artinskian-Kungurian	Li et al. 1980
Yakovlevia sinuata Lee and Gu 1980	Wujiatong Fm., Helongjiang Prov., NE China	Artinskian-Kungurian	Li et al. 1980
Yakovlevia yujiagouensis (Lee and Gu 1980)	Lower Permian, Helongjiang Prov., NE China	Artinskian-Kungurian	Li et al. 1980
Yakovlevia martianovi (Lapina 1957)	The Urals and Russian Platform	M. Carboniferous-Early Permian	Kalashnikov 1980
Yakovlevia usualis (Duan and Lee 1985)	Zhesi Fm., Inner Mongolia, NE China	Artinskian-Kungurian	Li & Gu in Ding et al. 1985
Yakovlevia spinosa (Duan and Lee 1985)	Zhesi Fm., Inner Mongolia, NE China	Artinskian-Kungurian	Li & Gu in Ding et al. 1985
Yakovlevia borealis (Liu and Waterhouse 1985)	Zhesi Fm., Inner Mongolia, NE China	Artinskian-Kungurian	Liu & Waterhouse 1985
Yakovlevia convexus (Liu and Waterhouse 1985)	Zhesi Fm., Inner Mongolia, NE China	Artinskian-Kungurian	Liu & Waterhouse 1985
Yakovlevia sp.	Honshu Island, Japan	Kungurian	Horikoshi et al. 1987
Yakovlevia sp.	Kitakami Mountains, Japan	Middle Permian	Tazawa 1987

Table 1 (continued).

ornament, between the two genera. This species is, in particular, characterised by costellae that are coarser than those found in typical *Yakovlevia* but finer than those seen in *Sajakella formosa* Nasikanova (in Grigor'yeva & Nasikanova 1968), the type species of *Sajakella*. Apart from *Yakovlevia martianovi*, only two other species are known from the Upper Carboniferous, *Y. artiensis* (Chernyshev 1889) and *Y. pseudoartiensis* (Stuckenberg 1905), both persisting into the Lower Permian and confined to the Urals and the Russian Platform (Table 1).

Yakovlevia diversified in the Early Permian (two-fold Permian System), especially in the Late Artinskian to Kungurian times when it spread across the Boreal Realm as well as penetrating into the western coast of North America, Central America (Mexico), north and northeast China, Sikhote Alin, and central and northeast Japan (Fig. 2). In northeast China, Sikhote Alin, and Japan, *Yakovlevia* species of this age are found in association with not only other typical Boreal elements such as *Sowerbina* Fredericks, *Timaniella* Barchatova, and *Tumarinia* Solomina & Grigor'yeva, but also typical warm-water Tethyan genera including *Tyloplecta* Muir-Wood & Cooper, *Compressoproductus* Sarycheva, *Spino-*

marginifera Huang, and *Permundaria* Nakamura, Kato & Choi (Tazawa 1991; Shi & Archbold 1995). This peculiar mixed-type fauna is very characteristic for the mid-Permian (Late Artinskian to Kungurian/Ufimian) of the north China–Japan–Sikhote Alin region, or the Inner Mongolia-Japanese Transitional Zone (Tazawa 1991). However, the origin of this mixed or transitional (i.e. transitional between the Boreal and Tethyan Realms) fauna remains unclear although we have elsewhere (Shi et al. 1995) suggested that it may have been formed in an intracratonic seaway on a newly formed stationary margin of the North China Block as a consequence of faunal migration from both the Cathaysian Province of the Tethyan Realm in the south and the Verkolyman Province of the Boreal Realm in the north (Fig. 3).

Similarly, the juxtaposed occurrences of *Yakovlevia* in both the Cordilleran Province (Yancey 1975), the McCloud Belt or Province (Miller 1987; = 'Exotic Province' of Yancey 1975), and the Grandian Province (Yancey 1975) of western North America (Fig. 3) is also puzzling. According to Yancey (1975) and Stevens (1985), both the Cordilleran and Grandian provinces were situated on the stable North American craton during the Permian and their palaeobiogeographical
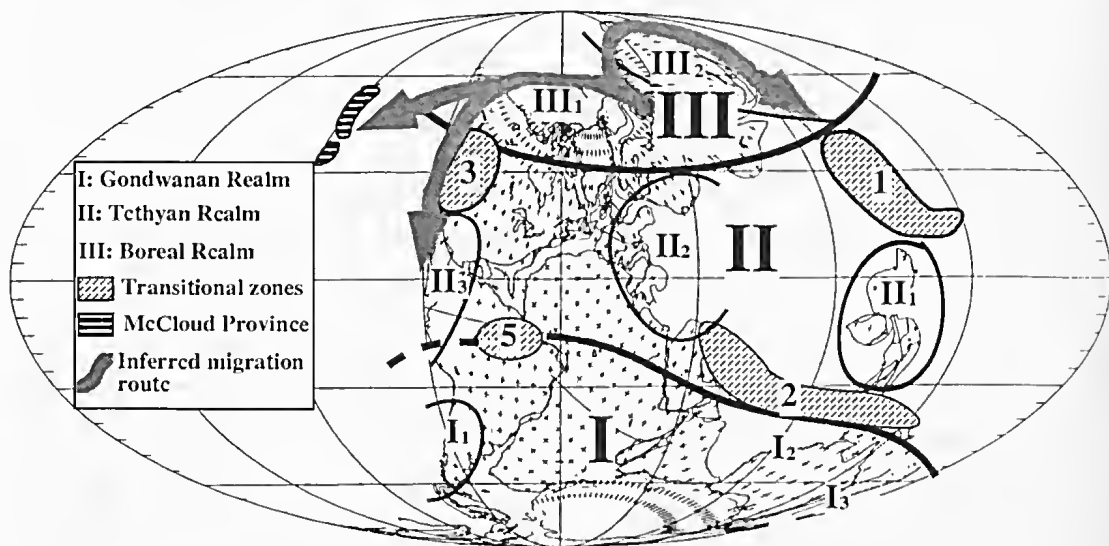
Fig. 3. Permian biogeographical realms and provinces and possible migration route of *Yakovlevia* during the Permian, modified from Shi et al. (1995) with the base map adopted from Scotese & MecKerrow (1990). The Permian biotic provinces are as follows: 1 = Northern Transitional Zone (Sino-Mongolian Province); 2 = Southern Transitional Zone (Cimmerian Province); 3 = Cordilleran Province; I₁ = Paratinan Province, I₂ = Westralian Province, I₃ = Austrazean Province; II₁ = Cathaysian Province, II₂ = West Tethys Province, II₃ = Grandian Province; III₁ = West Arctic Province; III₂ = Verkolyma Province.

differentiation may have resulted from the palaeo-latitude-related temperature differences. Thus, the occurrences of *Yakovlevia* in these two provinces may be explained using the scenario proposed by Ustritskiy (1968). He suggested that during the Late Carboniferous to Early Permian there were broad connections between the Arctic sea and the Tethys, one of which may have been via eastern Alaska–Yukon southward along the western margin of the North American craton to south-western United States–Central America. It was probably through this seaway connection that some typical Boreal elements including *Yakovlevia* migrated southwards into both the Cordilleran and Grandian provinces (Fig. 3).

However, the same scenario cannot be invoked to account for the presence of *Yakovlevia* in the McCloud Province (including such suspect terranes as Wrangellia, Grindstone and Eastern Klamath) because this province is now thought by many to have originated offshore and was separated from the North American craton by thousands of kilometres during the Permian (e.g. Stevens 1985; Stanley & Yancey 1990). This province contains a remarkable admixture of Boreal, Grandian, as well as Asian Tethyan faunal elements. The Asian Tethyan and Grandian components have been well recognised by previous studies (e.g. Stevens et al. 1990), presumably because of their abundance. However, the Boreal component has been largely overlooked. Among this category we may note the following brachiopod genera that have been described from central Oregon (Cooper 1957) and northern California (Coogan 1960): *Thule-productus* Sarycheva & Waterhouse, *Sowerbina* Fredericks, *Yakovlevia* Fredericks, *Septacamera* Stepanov, *Camerisma* (*Callaiapsida*) Grant, and *Spiriferella* Chernyshev. The origin of the McCloud Province has seen much recent debate and most workers now seem to agree that it represents a remanent of a Permian volcanic arc then located somewhere in the palaeo-Pacific, perhaps near the palaeo-Equator, with geographical proximities to both East Asia and North America (these proximities were necessary to account for the presence of both Asian Tethyan and Grandian elements) (e.g. Miller 1987; Stevens et al. 1990). Although this hypothesis appears to be supported by limited palaeomagnetic data (Mankinen et al. 1989) which indicate that the Eastern Klamath terrane was located at $17.8° \pm 8.4°$N latitude, the presence of the Boreal elements in the province is hardly explainable using this scenario. To account for the importance of the Boreal elements, an alternative explanation is required. Therefore, I suggest that it is probably more likely that the Eastern Klamath terrane and other terranes of the McCloud Province that contain both Boreal, Asian Tethyan and Grandian Permian faunas have originated in a more northerly position, perhaps in the palaeotemperate zone between palaeolatitudes 30° and 50°N, with geographical proximities to both East Asia, northeast Asia, and North America (Fig. 3).

YAKOVLEVIA TRANSVERSA ZONE FROM NORTHERN YUKON TERRITORY, WESTERN CANADA, AND ITS DISTRIBUTION IN NORTH AMERICA AND THE ARCTIC REGION

Fossils are abundant throughout the Permian marine sequences of the northern Yukon Territory, located in the Foreland Belt of western Canada (Fig. 4). Permian stratigraphy of this region was established by Bamber & Waterhouse (1971) and recently reviewed by Bamber et al. (1989). The marine Permian System comprises the Jungle Creek Formation in the lower part and the Tahkandit Formation in the upper, ranging in age from the Asselian to Wordian. Waterhouse (in Bamber & Waterhouse 1971) constructed a comprehensive biozonation scheme for the entire Permian succession based on brachiopod faunas, most of which are yet to be described. He proposed some 6 biozones for the Jungle Creek Formation and 4 for the overlying Tahkandit Formation. These zones were considered to be assemblage biozones. I (Shi 1994) have recently described the *Jakuto-productus verchoyanicus* Zone (formerly known as the *Jakutoproductus* Zone), of the Early Artinskian (Aktastinian) age, from the top of the Jungle Creek Formation. The present paper provides a review of another zone, the *Yakovlevia transversa* Zone [i.e. the *Yakovlevia* Zone (or Ey zone) of Waterhouse in Bamber & Waterhouse 1971] from the lower-middle part of the Jungle Creek Formation.

In northern Yukon territory, the *Yakovlevia transversa* Zone occurs above the *Tomiopsis–Attenuatella* Zone and below either the '*Attenu-atella*' Zone (the so-called '*Attenuatella*' is yet to be renamed as a new genus) or the *Tornquistia* Zone, and is distinguished overall by the pre-dominant occurrence of *Yakovlevia transversa* (Cooper) and absence of *Attenuatella* spp. that characterise the underlying *Tomiopsis–Attenuatella* Zone. The fauna of the *Yakovlevia transversa* Zone is large, comprising 57 of the 67 brachiopod species I (Shi 1991) described from the middle and upper parts of the Jungle Creek Formation, dominated by productids and to less extent by spiriferids.

Of the total 57 brachiopod species present in this zone, 20 are restricted to it, at least 8 were also found in the underlying *Tomiopsis–Attenuatella* Zone according to data in Waterhouse (in Bamber & Waterhouse 1971), and 28 range into overlying zones. In terms of abundance, short range, and wide distribution, the diagnostic elements of this zone include the following species: *Arctitreta* n. sp., *Komiella omolonensis* (Likharev), *Finibrinia* n. sp., *Tubersulculus maximus* Waterhouse, *Kutorginella yukonensis* Sarycheva & Waterhouse, *Rugivestis* n. sp., *Waagenoconcha permocarbonica* Ustritskiy, *Calliprotonia inexpecta* (Cooper), *Reticulatia*

uralica (Chernyshev), *Antiquatonia cooperi* Shi, *Linoproductus dorotheevi* Fredericks, *Protoanidanthus* n. sp., *Yakovlevia transversa* (Cooper), *Rhynchopora magna* Cooper, *Spiriferella pseudodraschei* Einor, Syringothyrid? n. gen. et sp., *Domokhotia* n. sp., *Spirelytha fredericksi* Archbold & Thomas, and a bivalve *Acanthopecten licharewi* (Fredericks). Of these characteristic constituents, the nominal species, *Yakovlevia transversa*, is most widespread and abundant, as well as very diagnostic in morphology, and thus may be easily recognized in the field. This species is not restricted to this zone, however; it has also been found
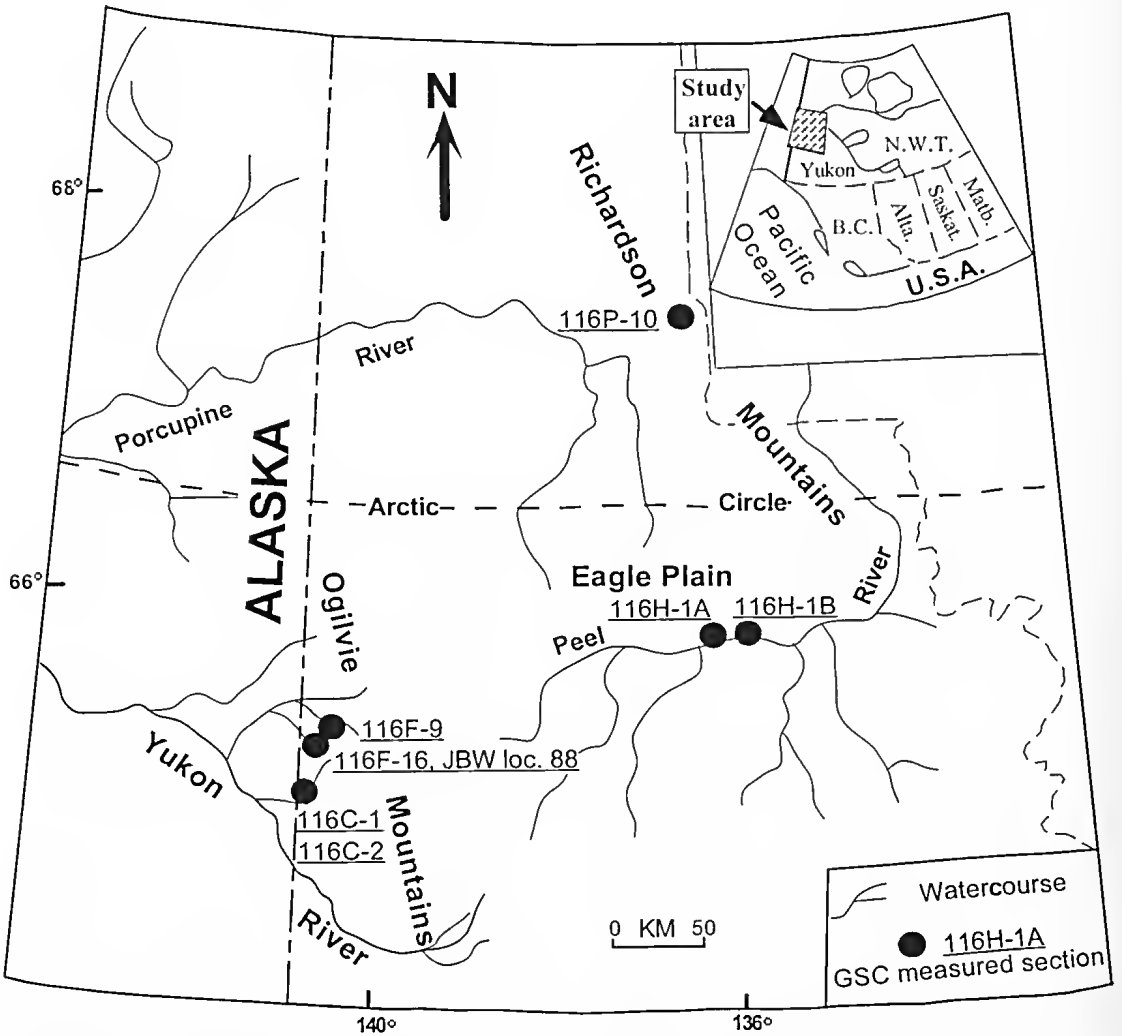
Fig. 4. Map showing area of study and the location of Geological Survey of Canada (GSC) sections referred to in the text and where the *Yakovlevia transversa* Zone has been recorded.

sporadically in the overlying '*Attenuatella*' and *Jakutoproductus verchoyanicus* zones (Shi 1991, 1994).

The base of the *Yakovlevia transversa* Zone is defined by the disappearance of species of *Attenuatella* and the first appearance of such species as *Arctitreta* n. sp., *Rugivestis* n. sp., *Protoanidanthus* n. sp., *Spirelytha fredericksi*, and the co-occurrence of abundant *Fimbrinia* n. sp., *Kutorginella yukonensis*, *Yakovlevia transversa*, and *Rhynchopora magna*. The upper boundary approximately corresponds to the lower limit of the overlying '*Attenuatella*' Zone, which is marked by the restricted and abundant occurrence of this new ambicoeliid species; or the *Tornquistia* Zone characterised by *Tornquistia* sp. and a distinct ammonoid fauna described by Nassichuk (1971).

The reference section of the *Yakovlevia transversa* Zone is designated at GSC section 116H-1A

along the Peel River, southern Eagle Plain (Figs 4 and 5). The lithostratigraphy of this section has been fully described by Bamber (1972). In this section, the *Yakovlevia transversa* Zone occurs from approximately 24 m to 210 m above the base of the Jungle Creek Formation and is identified by more than 20 species (see Fig. 5), notably *Komiella omolonensis* (Likharev), *Waagenoconcha permocarbonica*, *Kutorginella yukonensis*, *Kochiproductus porrectus* (Kutorga), *Yakovlevia transversa*, *Camerisma* (*Callaiapsida*) *pentameroides* (*Chernyshev*), *Spiriferella saranae* (Verneuil), *Alispiriferella ordinaria* (Einor), *Tomiopsis ovulum* Waterhouse, and *Dielasma brevicostatum* Cooper.

The *Yakovlevia transversa* Zone appears to be widely distributed in the northern Yukon Territory. In addition to the reference section, this zone has also been recorded from the GSC sections 116F-9, 116F-16, 116C-1, and 116C-2 in the northern
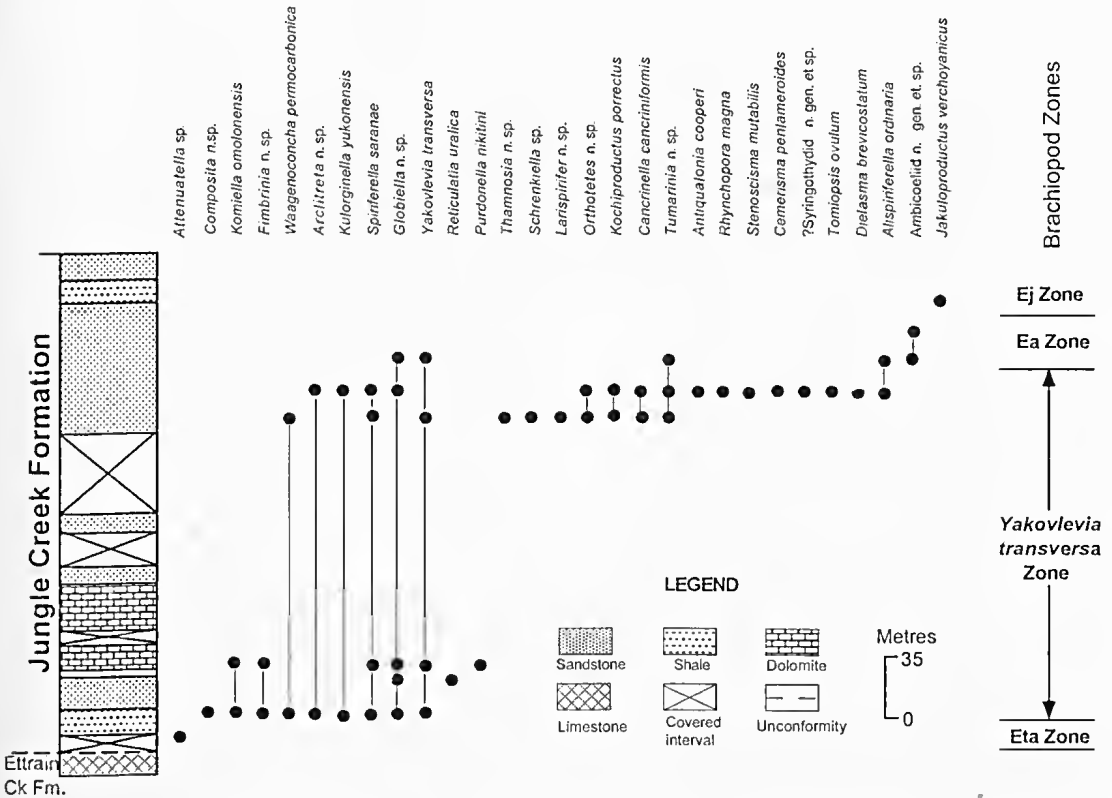
Fig. 5. Reference section of the *Yakovlevia transversa* Zone (GSC section 116H-1A), Peel River, southern Eagle Plain, northern Yukon Territory. The succession of the brachiopod zones as proposed by Waterhouse (in Bamber & Waterhouse 1971) are as follows: Eta Zone — *Tomiopsis-Attenuatella* Zone; Ea Zone — '*Attenuatella*' Zone (the so-called '*Attenuatella*' is yet to be renamed as a new genus); Ej Zone — *Jakutoproductus verchoyanicus* Zone (this zone has been fully described recently by Shi 1994).

Ogilvie Mountains, section 116H-1B on the Peel River of southern Eagle Plain, and in the section 116P-10, northern Richardson Mountains (Fig. 4).

Overall, the brachiopods of the *Yakovlevia transversa* Zone appear to indicate a general Sakmarian age, most likely Early Sakmarian (Tastubian) in view of both brachiopods and an ammonoid species found in the same zone. Many species characteristic for this zone are also common in the Sakmarian Stage of the Urals, as summarized by Miloradovich (1949), Stepanov (1951), and Kalashnikov (1986), notably *Reticulatia uralica*, *Tubersulculus maximus* (probably conspecific with *Productus pseudoaculeatus* Krotov of Chernyshev 1902), *Kochiproductus porrectus*, *K. saranaeanus* Fredericks, *Linoproductus dorotheevi* [= *Linoproductus cora* (not d'Orbigny) of Chernyshev and also comparable with *L. rhiphaeus* Stepanov), *Cancrinella cancriniformis* (Chernyshev), and *Purdonella nikitini* (Chernyshev). Of these species, *Linoproductus rhiphaeus* was cited to be confined to the Tastubian in the Urals (Kalashnikov 1986, p. 90), and *Reticulatia uralica* and *Tubersulculus maximus* first appeared in the Tastubian in the Urals (Stepanov 1951, p. 104). *Yakovlevia transversa* is very close to *Y. mammatiformis* (Fredericks), a species that Kalashnikov (1986) figured as one of the leading forms of the Sakmarian Stage in the Urals. *Y. mammatiformis* is also characteristic for the Sezim Suite of the Pechora Basin, north Urals (Ifanova 1972; Kalashnikov in Meyen 1983), which has been well dated Late Asselian to Sakmarian by ammonoids (Andrianov 1985).

Two taxa of the *Yakovlevia transversa* Zone are identical to or closely resemble species from the Southern Hemisphere and also support a general Sakmarian age for this zone. *Globiella* n. sp. is similar to *Globiella umariensis* (Reed) from the Umaria Beds of Peninsula India, of Early Sakmarian (Tastubian) age (Archbold 1983). The second species, *Spirelytha fredericksi* Archbold & Thomas, is confined to the *Yakovlevia transversa* Zone in northern Yukon Territory. The same species is elsewhere known only from the Late Sakmarian (Sterlitamakian) fauna of the Callytharra Formation in Western Australia (Archbold & Thomas 1984).

The ammonoid species, *Tabantalites bifurcatus* Ruzhencev (1952), was reported by myself (Shi 1991) from GSC loc. 57053 (assigned to the *Yakovlevia transversa* Zone) in the section 116F-16 in the northern Ogilvie Mountains. In south Urals, *T. bifurcatus* is known only from the upper Asselian and lower Sakmarian (Tastubian) strata (Ruzhencev 1952).

Thus, by judging from both brachiopods and the ammonoid summarized above, it seems most likely that the *Yakovlevia transversa* Zone is of Early Sakmarian (Tastubian) age. This age assignment would be consistent with the Late Asselian age of the underlying *Tomiopsis–Attenuatella* Zone proposed by Waterhouse & Waddington (1982).

Beyond the Yukon Territory, the *Yakovlevia transversa* Zone is found to be correlative with a few Permian faunas in western North America and the Arctic. Logan & McGugan (1968) listed and partially described a brachiopod fauna from the Telford Formation in southeastern British Columbia, including the following identifiable species: *Kutorginella* sp. cf. *K. neoinflatus* (Likharev), *Anidanthus eucharis* (Girty), *Yakovlevia* sp. cf. *Y. greenlandica* Dunbar (probably *Y. transversa*), *Spiriferella saranae*, and *Alispiriferella* sp. cf. *A. ordinaria*, *Purdonella* sp. cf. *P. nikitini*, and *'Spirifer' osborni* Harker. As a whole, this assemblage appears to suggest a generalized, perhaps condensed or latitudinally differentiated, correlation with faunas from the Yukon Jungle Creek Formation, more likely the *Yakovlevia transversa* Zone. A more positive correlation may be made between the Yukon *Yakovlevia transversa* Zone with the fauna from the Lower Permian 'Formation B' in the Buttle Lake area of Vancouver Island (Yole 1963). Of some 15 brachiopod species found from this unit, 9 are shared by the Yukon *Yakovlevia transversa* Zone, including species characteristic of this zone such as *Calliprotonia inexpecta*, *Kochiproductus porrectus*, *Antiquatonia cooperi*, *Sowerbina bullocki* (Nelson & Johnson), *Yakovlevia transversa*, *Neospirifer* sp., *Rhynchopora magna*, *Spiriferella saranae*, and *Camerisma (Callaiapsida) pentameroides*.

There seems to exist a great similarity of the Yukon Jungle Creek brachiopod faunules to brachiopods from the upper part of the Coyote Butte Formation in central Oregon, northwestern United States, described by Cooper (1957). Cooper considered the Oregon brachiopod fauna most likely to be Roadian or Kungurian in age, a conclusion that seems to be also in agreement with the age determination from fusulinids and sparse conodonts found from the same formation (Wardlaw et al. 1982). However, this age is inconsistent with the Asselian to Early Artinskian age assigned to the Yukon Jungle Creek faunules. There are no single species found in common between the Roadian brachiopod fauna of West Texas and the Coyote Butte fauna. On the other hand, there are ten species from the Oregon fauna that have also been found in the Yukon Jungle Creek faunules, of which nine are known from the *Yakovlevia*

transversa Zone: *Krotovia pustulata* (Keyserling); *Calliprotonia inexpecta, Kochiproductus porrectus*; *Waagenoconcha parvispinosa* Cooper, *Antiquatonia cooperi, Linoproductus dorotheevi*; *Yakovlevia transversa, Rhynchopora magna*, and *Spiriferella pseudodraschei*. Clearly, there is a need to reassess the biostratigraphical and palaeobiogeographical implications of the Oregon brachiopod fauna in the light of modern taxonomy and recent advances on the geology of surrounding areas, in order to resolve the discrepancy on the age determination and correlation of the Oregon fauna.

The *Yakovlevia transversa* Zone is also traceable at many Arctic localities but detailed correlation with these Arctic assemblages is hindered by the lack of modern revisions of the Arctic faunas. A large Permian brachiopod fauna was described by Likharev & Einor (1939) from a number of localities on Novaya Zemlya. The majority of species described were collected from the Barents Series on the western coast of the north island, between Sedov Bay and Russian Harbour. This fauna consisted of some 63 species, of which 5 are also found in the Yukon *Yakovlevia transversa* Zone: *Orthotichia morganiana* (Derby), *Kochiproductus saranaeanus, Reticulatia uralica, Spiriferella pseudodraschei*, and *S. saranae*. In addition, a few more species may be compared with representatives from the Yukon zone, including *Calliprotonia sterlitamakensis* Stepanov (close to Yukon *C. inexpecta*), *Schrenkiella schrenki* (Stuckenberg) (similar to Yukon *Schrenkiella* sp.), and *Rhynchopora nikitini* (Chernyshev) (comparable with Yukon *R. magna*). On the other hand, the Barents Series also contains *Thuleproductus arcticus* (Whitfield) and *Anemonaria pseudohorrida* (Wiman), which normally occur in younger Permian (Kungurian or younger) deposits in the Arctic region. Thus, the Barents Series may have a longer age range than the Yukon *Yakovlevia transversa* Zone; or the listed fauna of the Barents Series may have been mixed from two or more assemblages of different age.

Permian brachiopods of the Taimyr Peninsula were described by Einor (1939, 1946) and Ustritskiy & Chernyak (1963). The fauna from the upper Turuzov Horizon, assigned an Asselian to Sakmarian age by Ustritskiy & Chernyak (1963), appears to be at least in part correlative with the Yukon *Yakovlevia transversa* Zone. Species common to both areas are *Dyoros (Dyoros) pseudotrapezoidalis* (Miloradovich), *Fimbrinia* n. sp., and *Waagenoconcha permocarbonica*.

The brachiopod fauna from the Afonin Horizon of the Verchoyan Mountains in northeast Siberia, described by Kashirtsev (1959) and Abramov &

Grigor'yeva (1988), appears to be in part correlated with the Yukon *Yakovlevia transversa* Zone, with the following species in common or closely comparable: *Anidanthus*? *sarytchevae* Zavodovskiy (close to Yukon *Protoanidanthus* n. sp.), *Fimbrinia* n. sp., *Kochiproductus porrectus*, 'Marginifera' *peregrina* (not Fredericks) (in part conspecific with Yukon *Rugivestis* n. sp.), and *Cancrinella cancriniformis* (Chernyshev). A similar fauna has also been reported from the Irbichan Horizon of the Kolyma–Omolon Massif in northeast Siberia (Zavodovskiy & Stepanov 1971), with the following species shared with or closely related to those of the Yukon *Yakovlevia transversa* Zone: *Overtonia gijigensis* Zavodovskiy (close to Yukon *Fimbrinia* n. sp.), *Cancrinella cancriniformis, Anidanthus aagardi* (not Toula) (close to Yukon *Protoanidanthus* n. sp.), *Yakovlevia mammatiformis* (close to Yukon *Y. transversa*), *Kitakamithyris stepanovi* (Zavodovskiy) (comparable with Yukon *Spirelytha* sp.).

The *Yakovlevia transversa* Zone can be traced further north in Spitsbergen, where correlative faunas occur in the upper Wordiekammen Limestone (see Gobbett 1964) in central Vestspitsbergen and in the Treskelodden Beds on the northeastern coast of Hornsund, southwestern Vestspitsbergen (Czarniecki 1969). With both Spitsbergen assemblages the Yukon zone shares *Reticulatia uralica* (Chernyshev), *Linoproductus dorotheevi* (Fredericks), and *Cancrinella singletoni* Gobbett.

SYSTEMATIC PALAEONTOLOGY

Order PRODUCTIDA Sarycheva & Sokolskaya, 1959

Superfamily LINOPRODUCTACEA Stehli, 1954
(nom. transl. Waterhouse, 1978; ex.
LINOPRODUCTIDAE Stehli, 1954)

Family YAKOVLEVIIDAE Waterhouse, 1975
(nom. transl. Waterhouse, 1978; ex.
YAKOVLEVIINAE Waterhouse, 1975)

Diagnosis. Subquadrate to transverse shells with wide hinge margin and well demarcated ears and abrupt geniculation; visceral disc flattened to gently concavo-convex; shell surface capillate to costellate; ventral valve normally with 4 basic, large halteroid spines: one on each ear and one on each side of sulcus just anterior to the venter, and rare, scattered body spines; no dorsal spines. Marginal ridges absent to very weakly developed.

Genera included and discussion. The following genera are included in the family: *Sajakella* Nasi-

kanova (in Sarycheva et al. 1968), *Yakovlevia* Fredericks (1925), *Duartea* Mendes (1959), and *?Paramuirwoodia* Zhang (in Zhang et al. 1983). Inclusion and the validity of *Paramuirwoodia* is questionable. This genus, with type species *P. quadrata* Zhang (in Zhang et al. 1983), is characterised by a subquadrate to slightly transverse outline, abrupt geniculation, costellate shell surface, and a pair of large halteroid spines on umbonal slopes of the ventral valve. Apart from the spine pattern, all other characteristics of this genus can be closely compared with those of *Productus batesianus* Derby (1874), the type species of *Duartea* (note that *Duartea* has 4 large halteroid spines, like *Yakovlevia*). In addition, both type species also have weakly developed marginal ridges in the dorsal valve (see Zhang in Zhang et al. 1983: pl. 133, fig. 1d; Mendes 1961: fig. 16). Although Zhang defined *Paramuirwoodia* as possessing only one pair of halteroid spines on umbonal slopes of the ventral valve (this pattern is unlike any other yakovleviid genus), at least one additional large halteroid spine base is clearly shown on one side of the ventral trail next to the sulcus in *Paramuirwoodia quadrata* (see Zhang in Zhang et al. 1983: pl. 133, fig. 1a). If this observation is correct, the overall spine pattern of *Paramuirwoodia* seems more like that of *Paucispinifera* than that of *Yakovlevia*; however, the exact nature of the halteroid spines of *Paramuirwoodia* remains to be clarified, preventing any positive determination at the present as to its familial status and relationship with *Duartea*.

The combination of spine pattern, capillate to costellae exterior, flat to gently concavo-convex visceral disc, and the abruptly geniculated trail make the family Yakovleviidae unique within the Linoproductacea. No other linoproductaceans seem to have the four basic large halteroid spines symmetrically distributed on the ventral valves.

Genus **Yakovlevia** Fredericks, 1925

Yakovlevia Fredericks 1925: 7. — Muir-Wood & Cooper 1960: 323. — Sarycheva et al. 1960: 233. — Kotlyar 1961: 459. — Muir-Wood 1965: H506. — Grant in Brabb & Grant 1971: 16. — Cooper & Grant 1975: 1177. — Lazarev 1990: 85.
Muirwoodia Likharev 1947: 187. — Dunbar 1955: 111. — Muir-Wood & Cooper 1960: 322. — Muir-Wood 1965: H506. — Lazarev 1990: 85.

Diagnosis. Medium to large transverse Yakovleviidae, shell surface capillate to finely costellate, usually with a row of spines along hinge margin of ventral valve; marginal ridges absent to weakly developed.

Discussion. *Yakovlevia* is similar to *Sajakella* and *Duartea* in having the 4 basic large halteroid spines on the ventral valve, lack of dorsal spines, and an abrupt geniculation, but the latter two usually have notably coarser costellae. In addition, *Sajakella* seems to have relatively more finer body spines scattered on the ventral valve, and *Duartea* lacks a hinge row of spines according to Muir-Wood (1965) and is usually more quadrate than transverse in outline, and its ears are also less demarcated. *Paramuirwoodia*, subjected to the clarification of its halteroid spines on the ventral valve, can be distinguished from *Yakovlevia* also by its coarser costellae, more quadrate outline, and the lack of a row of hinge spines.

Geographic distribution. Arctic, western North America, Mexico, north and northeast China, Japan, and eastern Russia (see Table 1, Fig. 2).

Stratigraphic distribution. Middle Carboniferous to Kazanian (see Table 1).

Yakovlevia transversa (Cooper, 1957)

Fig. 6A–O

Muirwoodia transversa Cooper 1957: 39, pl. 5A, figs 1–13.
Yakovlevia sp. Waterhouse in Bamber & Waterhouse 1971: pl. 14, figs 2–5; pl. 15, fig. 1; pl. 16, fig. 7.
Yakovlevia transversa. — Nelson & Nelson (partim.) 1985: pl. 1, figs 10–11; not fig. 12.

Fig. 6. A–O, *Yakovlevia transversa* (Cooper, 1957). A, posterior view of ventral valve, GSC 97153 from GSC loc. 53946, GSC section 116C-1. B, 1, posterior and anterior views of ventral valve, GSC 97045 from GSC loc. 53721, section 116H-1B. C, posterior view of dorsal external mould, GSC 97148 from GSC loc. 53703, section 116H-1A. D, latex cast of dorsal internal mould, GSC 97052 from JBW loc. 88. E, ventral internal mould, GSC 97152 from JBW loc. 88. F–G, ventral internal mould and latex cast, GSC 97051 from JBW loc. 88. H, latex cast of dorsal internal mould, GSC 97055, JBW loc. 88. J, posterior view of ventral valve, GSC 97046 from GSC loc. 56972, section 116F-16. K, lateral view of ventral internal mould, GSC 97053 from GSC loc. 53860, section 116P-10. L, anterior view of ventral valve, GSC 97049 from GSC loc. 53721, section 116H-1B. M, posterior view of ventral valve, GSC 97047 from GSC loc. 53721, section 116H-1B. N, lateral view of ventral valve, GSC 97147 from GSC loc. 53703, section 116H-1A. O, anterior view of ventral valve, GSC 97054 from GSC loc. 56972, section 116F-16. All specimens are in natural size.
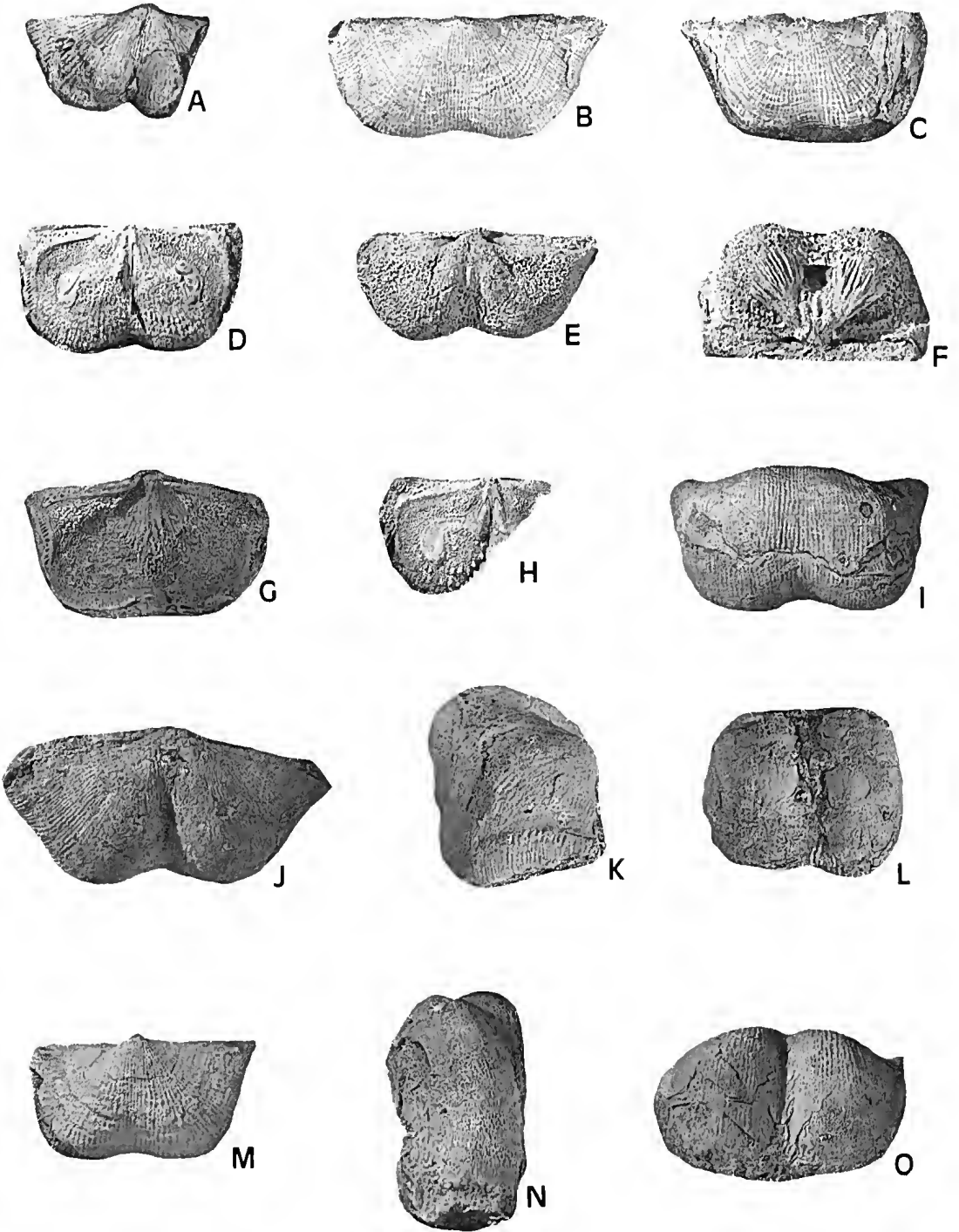
Holotype. USNM 125339 figured in Cooper (1957) in pl. 5A, figs 2 and 3 from the Coyote Butte Formation, central Oregon, United States.

Diagnosis. Large transverse *Yakovlevia* with flattened to gently convex ventral visceral disc; sulcus and fold well developed at maturity; 5–7 costellae in 5 mm on ventral trail.

Referred material. Eight specimens with valves conjoined from GSC loc. 53703, section 116 H-1A; 6 conjoined specimens from GSC loc. 53721, section 116H-1B; 10 ventral valves and 5 dorsal external moulds from GSC loc. 53860, section 116P-10; 4 ventral valve and 1 dorsal external mould from GSC loc. 53862, section 116P-10; 1 ventral valve from GSC loc. 53946, section 116C-1; 5 ventral valves and 3 dorsal valves from GSC loc. 56972, section 116F-16; 3 ventral valves, 1 ventral internal mould, 3 dorsal external moulds, 4 dorsal internal moulds and 2 complete shell specimens from JBW loc. 88, near section 116F-16 (see Fig. 4 for locations of the GSC sections).

Description. Shell medium to moderately large with transverse outline; widest at hinge line. Ventral valve abruptly geniculated at angle between 60° and 80°; visceral disc flat to gently convex, subrectangular to trapezoidal in shape; umbo tiny, flat; no prominent umbonal slopes; ears large, well extended, but poorly differentiated from umbo, slightly to moderately rounded in cross section; hinge usually slightly wider than midwidth; cardinal extremities acute at 80° on average; angle between hinge margin and lateral margin of visceral disc ranging from 55° to 65°; trail approximately 1.5 as long as visceral disc when completely preserved, subquadrate to slightly clonsulcus distinct in all ventral specimens, but varying in depth and distance from umbo in specimens even from one locality, usually commencing 2–4 mm from umbo with sulcal angle at 40° to 50°, deepening and widening forwards, strongest over geniculation area with angular floor, slightly shallower anteriorly and floor more broadly rounded; flanks bounding sulcus high and narrowly rounded in transverse section with nearly vertical lateral slopes. Costellae well defined, low and rounded, 8 in 5 mm at 6 mm from umbo (Fig. 6M), 5–7 in 5 mm on trail (Fig. 6I), anteriorly increasing by intercalation, separated by narrow interspaces, slightly converging in sulcus in some specimens; rugae much weaker than costellae, low and rounded, 1–2 per mm, better defined on inner ears, slightly crossing costae; reticulation indistinct. Spines few, well differentiated; coarse strut spines usually measuring

1–1.5 mm in diameter, interrupting 2 or more costellae which continue forward in front of spine bases, slightly varying in number and position, but always with one pair from cardinal extremities, one and rarely two pairs on flanks bounding sulcus, none on lateral slopes, and rarely one in sulcus (Fig. 6L); finer spines comparatively more numerous, in row along hinge line and rare over trail and visceral disc, there arising from single costella, 0.5 mm in diameter.

Dorsal valve strongly concave, but visceral disc flat, trapezoidal; geniculation abrupt and narrow with angle between 50° and 75°; trail approximately as long as disc; fold variable as ventral sulcus, normally beginning at 3–5 mm in front of dorsal umbo, strongest over middle valve, crest rounded. Costellae similar to those on ventral valve; but rugae slightly stronger and more regularly defined, confined to visceral disc, about 5–7 in 5 mm, crossing costellae to form more prominent, at times well defined, reticulation in visceral disc; no spines observed on dorsal valves. Shell pseudopunctate, preserved as fine pits on worn surface (Fig. 6N).

Ginglymus not preserved; transverse band along posterior margin of both valves distinct in many specimens, 3–4 mm in diameter, irregularly pitted on ventral side and matched by tubercles on dorsal side, extending laterally across ears to lateral margins, there replaced by laterridges; lateral ridges striated and not reaching anterior margin.

Ventral muscle field deeply depressed just below transverse band, triangular in shape, posteriorly narrower and extending across transverse band, leaving small, smooth triangular opening simulating delthyrium, encircled by low ridges; adductor platform raised, high, narrow and elongate, divided by very thin median groove in some specimens, slightly striate on anterior portion, posteriorly smooth; large diductor scars on each side, deeply depressed below valve floor, flabellate, posteriorly smooth, anteriorly marked by distinct radial grooves and ridges; rest of valve floor densely granulate and pitted, stronger toward anterior margin.

Dorsal adductor scars small, slightly raised and dendritic, oval in shape; brachial ridges distinct with slightly recurved anterior portions, smooth inside loops; median septum low between adductor scars, extending slightly beyond midand ending with high anterior; floor irregularly granulate and pitted; 2–3 concentric rows of small endospines in front of brachial ridges and median septum.

Measurements. Width ranges from 30 to 47 mm, length 18 to 88 mm, height 15 to 19 mm, and cardinal angle 70° to 80°.

Comparisons. The holotype of *Yakovlevia transversa* (Cooper 1957) from the Coyote Butte Formation of central Oregon has a slightly deeper and longer sulcus than some of the Yukon specimens, but this feature is variable in the Yukon collections. Smaller specimens usually have a shallower sulcus (e.g. Fig. 6M). Larger and more transverse specimens possess a slightly deeper and longer sulcus (Figs 6J, O) comparable with that of the Oregon types. The two specimens figured as *Y. transversa* by Nelson & Nelson (1985) seem to be conspecific, but the ventral internal mould figured in their fig. 12 as the same species seems to have been mislabelled; it is perhaps a ventral internal mould of *Purdonella* Reed or ally, because it has long subparallel adminicula and a well impressed, elongate muscle field; this is not like any of the ventral interiors of *Yakovlevia transversa* from northern Yukon Territory.

Y. mammata (Keyserling 1846: p. 206, pl. 4, figs 5, 5a, b) and *Y. mammatiformis* (Fredericks 1926: p. 87, pl. 3, figs 4–6) are the two species closest to *Y. transversa*. The first was originally described from the possibly Sakmarian fauna of the Urals and has now been widely reported from chiefly Lower Permian (Asselian to Kungurian) in the Russian Arctic, Arctic Canada, and northeast China. The type material of this species is similar to some small specimens of the present species, with a shallow sulcus. Types of *Y. transversa* and most Yukon hypotypes are much larger and more transverse than *Y. mammata* and have a deeper sulcus. *Yakovlevia mammatiformis* from the Sakmarian beds in Kejim Terovey River of Timan, appears to be closer to *Y. transversa* in general appearance. The Russian types are poorly preserved but do show a large size, a more transverse outline, and coarser, more widely spaced costellae (see Abramov & Grigor'yeva 1983: pl. 10, figs 13, 14).

Occurrences. In the northern Yukon Territory, *Y. transversa* occurs throughout the Jungle Creek Formation, but is most abundant in the *Yakovlevia trasversa* Zone in the lower-middle part of the formation. Outside the Yukon Territory and apart from its occurrence at the type locality from the Coyote Butte Formation in central Oregon, *Y. transversa* is known also from the possibly Sakmarian fauna in southeast British Columbia (Nelson & Nelson 1985).

ACKNOWLEDGEMENTS

REFERENCES

ABRAMOV, B. S. & GRIGOR'YEVA, A. D., 1983. Biostratigrafiia i Brakhiopody Srednego i Verkhnego Karbona Verkhoyaniia [Biostratigraphy and Brachiopods of the Middle and Upper Carboniferous of Verchoyan]. *Akademiia Nauk SSSR, Paleontologicheskii Institut, Trudy* 200, 168 p, 32 pls. (In Russian.)

ABRAMOV, B. S. & GRIGOR'YEVA, A. D., 1988. *Biostratigrafiia i Brakhiopody Permi Verkhoyaniia* [Biostratigraphy and Brachiopods in the Permian of Verchoyan] Akademiia Nauk SSSR, Institut Geologii Yakutskogo Filiala Sibirskogo Otdeleniia, Paleontologicheskii Institut, Moscow, 208 p, 32 pls. (In Russian.)

ANDRIANOV, V. I., 1985. *Permiskie i Nekotorye Kamennougol'nye Ammonoidei Severo-vostoka Azii* [Permian and Some Carboniferous Ammonoids of North-eastern Asia]. Nauk, Novosibirsk, 186 p. (In Russian.)

ARCHBOLD, N. W., 1983. Studies on Western Australian Permian brachiopods. 3. The family Linoproductidae Stehli 1954. *Proceedings of the Royal Society of Victoria* 95(4): 237–254.

ARCHBOLD, N. W. & THOMAS, G. T., 1984. Permian Elythidae (Brachiopoda) from Western Australia. *Alcheringa* 8(4): 311–326.

BAMBER, E. W., 1972. Description of Carboniferous and Permian stratigraphic sections, northern Yukon Territory and northwestern District of Mackenzie (N.T.S. 106M; 116C, F, G, H, I, J, P; 117A, B, C). *Geological Survey of Canada, Paper* 72-19, 161 p.

BAMBER, E. W., HENDERSON, C. M., JERZYKIEWICZ, J., MAMET, B. L. & UTTING, J., 1989. A summary of Carboniferous and Permian biostratigraphy, northern Yukon Territory and northwest District of Mackenzie. In Current Research, pt G. *Geological Survey of Canada, Paper* 89-1G: 13-21.

BAMBER, E. W. & WATERHOUSE, J. B., 1971. Carboniferous and Permian stratigraphy and palaeontology, northern Yukon Territory, Canada. *Bulletin of Canadian Petroleum Geology* 19(1): 9–250.

BARCHATOVA, V. P., 1970. Biostratigraphy of the Carboniferous and Lower Permian in northern Timan. *Trudy Vsesouznogo Neftianogo Nauchno-Issledovatel'skogo Geologorazvedochnogo Instituta (VNIGRI)* 283: 1–228. (In Russian.)

BLOME, C. D. & NESTELL, M. K., 1991. Evolution of a Permo-Triassic sedimentary mélange, Grindstone terrane, east-central Oregon. *Geological Society of America Bulletin* 103: 1280–1296.

BRABB, E. E. & GRANT, R. E., 1971. Stratigraphy and Paleontology of the revised type section for the Tahkandit Limestone (Permian) in east-central Alaska. *U.S. Geological Survey, Professional Paper* 703, 26 p, 2 pls.

CHERNYSHEV, F. N., 1889. Beschreibung des Central-Urals und des Westabhanges. In Allgemeine Geologische Karte von Russland, Blatt 139. *Trudy Geologicheskago Komiteta* 3(4), 393 p, 7 pls. (In Russian with German summary.)

CHERNYSHEV, F. N., 1902. Verkhnekamennougol'nye brahkiopody Urala i Timana (Upper Carboniferous brachiopods from the Urals and Timan. *Trudy Geologicheskago Komiteta* 104(2), 749 p, 63 pls. (In Russian and German.)

CLOUD, P. E., 1944. Permian brachiopods. In Geology and Paleontology of the Permian northwest of Las Delicias, southwestern Coahuila, Mexico. Pt 3, R. E. King, C. O. Dunbar, P. E. Cloud, Jr & A. K. Miller, eds. *Geological Society of America, Special Paper* 52: 49–69.

COOGAN, A. H., 1960. Stratigraphy and paleontology of the Permian Nosoni and Dekkas Formations (Bollibokka Group). *University of California Publications in Geological Sciences* 36(5): 243–316.

COOPER, G. A. 1953. Sponges, Brachiopoda, Pelecypoda, and Scaphopoda. In Permian Fauna at El Antimonio, Western Sonora, Mexico, G. A. Cooper, C. O. Dunbar, H. Duncan, A. K. Miller & J. B. Knight, eds. *Smithsonian Miscellaneous Collections* 119(2): 21–82.

COOPER, G. A., 1957. Permian brachiopods from central Oregon. *Smithsonian Miscellaneous Collections* 134(12): 1–79.

COOPER, G. A. & GRANT, R. E., 1975. Permian brachiopods of west Texas, III. *Smithsonian Contributions to Paleobiology* 19: 795–1921.

CZARNIECKI, S., 1969. Sedimentary environment and stratigraphical position of the Treskelodden Beds (Vestspitsbergen). *Prace Museum Ziemi* 16: 201–336.

DERBY, O. A., 1874. On the Carboniferous Brachiopoda of Itaitúba, Rio Tapajos, Prov. of Pará, Brazil. *Cornell University Science Bulletin* 1(2): 1–6.

DING, Y. J., XIAO, G.-Y., DUAN, C.-H., LI, W.-G., LIU, X.-L. & LIANG, Z.-F., 1985. Study on the Permian stratigraphy and fauna in Zhesi district, Nei Mongol Zizhiqu (Inner Mongolia). *Bulletin of the Tianjin Institute of Geology and Mineral Resources* 10: 1–244, 58 pls. (In Chinese with English summary.)

DUNBAR, C. O., 1955. Permian brachiopod fauna of central east Greenland. *Meddelelser om Grønland* 110(3): 1–169.

EINOR, O. L., 1939. Some brachiopods from the Lower Permian of Taimyr (Basin of the Piassina River). *Trudy Arkticheskogo Institut* 135: 1–135. (In Russian with English summary.)

EINOR, O. L., 1946. Brachiopods of the Lower Carboniferous and Lower Permian of Taimyr. *Gorno-Geologicheskogo Uralavleniia, Trudy* 26: 1–91. (In Russian with English summary.)

FREBOLD, H., 1937. Das Festungsprofil auf Spitzbergen, IV. Die Brachiopoden und Lamellibranchiatenfauna und die Stratigraphie des Oberkarbons und Unterperms. *Meddelelser om Grønland* 126(3): 1–97.

FREDERICKS, G. N., 1926. Materials for the study of the fauna from sandstone-argillite sequence in the Kejim-Terovey River. *Izvestiia Geologicheskogo Komiteta* 45(2): 81–95. (In Russian.)

GIRTY, G. H., 1910. The fauna of the Phosphate beds of the Park City formation in Idaho, Wyoming and Utah. *U.S. Geological Survey Bulletin* 436: 1–82.

GOBBETT, D. J., 1964. Carboniferous and Permian brachiopods of Svalbard. *Norsk Polarinstitutt Skrifter* 127: 1–201.

GRIGOR'YEVA, A. D. & NASIKANOVA, O. N., 1968. The Family Marginiferidae Stehli. In Brakhiopody Verkhnego Paleozoiia Vostochnogo Kazakhstana [Brachiopods of the Upper Palaeozoic of Eastern Kazkhstan], T. G. Sarytcheva, ed. *Akademiia Nauk SSSR, Paleontologicheskii Institut, Trudy* 121: 148–155. (In Russian.)

HARKER, P. & THORSTEINSSON, R., 1960. Permian rocks and faunas of Grinnell Peninsula, Arctic Archipelago. *Geological Survey of Canada, Memoir* 309: 1–89.

HORIKOSHI, E., TAZAWA, J.-L., NAITO, N. & KANEDA, J., 1987. Permian brachiopods from Moribu, north of Takayama City, Hida Mountains, central Japan. *Journal of the Geological Society of Japan* 93(2): 141–143.

IFANOVA, V. V., 1972. Permian brachiopods from the Pechora Basin. In Sredynekamennougol'nye i Permiskie Brakhiopody Vostoka i Severa Europeiskoi Chasti SSSR [Middle Carboniferous and Permian Brachiopods from Eastern and Northern European Part of U.S.S.R.], V. V. Ifanova & E. G. Semenova ed. Akademiia Nauk SSSR, Nauchnyi Sovet po Probleme 'Puti i Zakonomernosti Razvitiia Jivtnykh i Rastitel'nykh Organismov', Moscow, p. 72–161, 13 pls. (In Russian.)

KALASHNIKOV, N. V., 1980. *Brachiopods of the Upper Palaeozoic from European Part of North U.S.S.R.* Akademiia Nauk SSSR, Komi Filial Institut Geologii, Leningrad, 135 p., 39 pls. (In Russian.)

KALASHNIKOV, N. V. 1986. Phylum Brachiopoda. In Atlas Kharakternykh Kompleksov Permskoi Fauny i Flori Russkoi Platformy [Atlas of Characteristic Complexes of Permian Faunas and Flora in the Urals and Russian Platform], V. P. Gorskiy & M. A. Kalmykova, eds. *Vseouznyi Orena Lenina Nauchno-Issledvatel'skii Geologicheskii Institut, Trudy, new ser.* 331: 29–30. (In Russian.)

KASHIRTSEV, A. S., 1959. *Podevoi Atlas Fauny Permskikh Otlozhenii Severo-vostoka SSSR* [Field Atlas of Faunas in the Permian Deposits of Northeast U.S.S.R.]. Akademiia Nauk SSSR, Yakutskii Filial Sibirskogo Otdeleniia, Moscow, 85 p., 44 pls. (In Russian.)

KEYSERLING, A. F., 1846. Geognostiche Beobachtungen. In Wissenschaftliche Beobachtungcn auf einer Reise in das Pctschora-Land im Jahre 1843, A. G. Keyserling & P. von Krusenstern, eds. St Petersburg, carl Kray, p. 151–336, 22 pls.

KOTLYAR, G. B., 1961. On genus *Yakovlevia* Frederiks. *Doklady Akademiia Nauk SSSR* 140(2): 459–460.

LAPINA, N. N., 1957. Carboniferous brachiopods from the Pre-Urals. *Trudy Vsesouznogo Neftianogo Nauchno-Issledovatel'skogo Geologo-Razvedochnogo Instituta* 108: 3–132. (In Russian.).

LAZAREV, S. S., 1990. Evolutsiya i sistema produktid (Evolution and Systematics of productids). *Akademiia Nauk SSSR, Paleontologicheskogo Institut, Trudy* 242, 173 p., 40 pls. (In Russian.)

LI, L. & GU, F., 1976. Brachiopoda. In *Paleontological Atlas of Northern China (Inner Mongolia). Pt I. Palaeozoic*, Geological Publishing House, Beijing, p. 228–506, pls 138–184. (In Chinesc.)

LI, L., GU, F. & SU, Y.-Z., 1980. Carboniferous and Permian Brachiopoda. In *Paleontological Atlas of Northern China. Palaeozoic Volume*, Geological Publishing House, Beijing, p. 327–429, pls 145–180. (In Chinese.)

LIAO, Z.-T., 1979. Uppermost Carboniferous brachiopods from western Guizhou. *Acta Palaeontologica Sinica* 18(6): 527–546. (In Chinesc.)

LIKHAREV, B. K., 1960. Uppcr Permian Brachiopoda of the southern Primorye and ccrtain single-age faunas of other regions of castcrn Asia. *Doklady Akademiia Nauk SSSR* 132(1–6): 483–485.

LIKHAREV, B. K., 1947. On thc ncw subgenus *Muirwoodia* of the genus *Productus* Sowcrby. *Doklady Akademiia Nauk SSSR* 57(2): 187–190.

LIKHAREV, B. K. & EINOR, O. L., 1939. Matcrials for the study of the Upper Palacozoic faunas of Novaya Zcmlya. Brachiopoda. *Trudy Arkticheskogo Nauchno-Issledovatel'skogo Instituta* 127, 245 p., 25 pls. (In Russian with English summary.)

LIKHAREV, B. K. & KOTLYAR, G. V., 1978. Permian brachiopods from southern Primoryc. In *Verkhnii Paleozoi Severo-Vostochnoi Asii*, L. 1. Popeko, ed. Akademiya Nauk SSSR, Dal'nevostochnyi Nauchnyi Tscntr Institut Tektonik i Geofiziki, Vladivostok, p. 63–99, pls 19–21.

LIU, F. & WATERHOUSE, J. B., 1985. Permian stratigraphy and brachiopods of Zhesi district of Damao County, Nei Mongol (Inner Mongolia) Autonomous Region, China. *University of Queensland, Department of Geology Papers* 11(2): 44 p., 12 pls.

LOGAN, A. & MCGUGAN, M., 1968. Biostratigraphy and faunas of the Pcrmian Ishbel Group, Canadian Rocky Mountains. *Journal of Paleontology* 42(5): 1123–1139.

MANKINEN, E. A., IRWIN, E. P. & GROMME, C. S., 1989. Paleomagnctic study of thc Eastern Klamath Terrane, California, and implications for the tectonic history of the Klamath Mountains Province. *Journal of Geophysical Research* 94: 10444–10472.

MENDES, C., 1959. Chonetacea e Productacea Carbon-

iferos da Amazônia. *Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo* 236 (Geol. vol. 17): 1–83.

MENDES, C., 1961. Notes suplementares s-bre os braquilpodes Carboniferos da Amaz-nia. *Boletim da Sociedade Brasileira de Geologia* 10(1): 24.

MEYEN, S. V., ed., 1983. *Paleontologicheskii Atlas Permskikh Otlozhenii Pechorskogo Ugol'nogo Basseina* [Palcontological Atlas of the Permian Deposits in Pcchora Coal Basin]. Akadcmiia Nauk SSSR Kim Filial Institut Geologii, Nauk, Leningrad, 258 p., 59 pls. (In Russian.)

MILLER, M. M., 1987. Dispcrsed remnants of a northeast Pacific fringing arc: Upper Palaeozoic terrane of Pcrmian McCloud faunal affinity, western U.S. *Tectonics* 6(6): 807–830.

MILORADOVICH. B. V., 1949. On the vertical extent of Upper Carboniferous and Lower Permian brachiopods from the Ufa Platform. *Izvestiia Akademiia Nauk SSSR, geologii ser.*, 1: 53–66.

MINATO, M. & TAZAWA, J.-L., 1977. Fossils of the Huentelauquén Formation at the locality F, Coquimbo Provincc, Chile. In *Comparative studies on the Geology of the Circum-Pacific Orogenic Belt in Japan and Chile, 1st Report*, T. 1shikawa & L. Aguirre, eds, Japan Society for the Promotion of Scicnce, Tokyo, p. 95–112, 3 pls.

MIRONOVA, M. G., 1964. Contributions to the knowledge of Early Pcrmian brachiopods of the Pechora Basin. *Voprosy Paleontologii* 4: 85–99. (In Russian.)

MIRONOVA, M. G., 1967. *Late Carboniferous brachiopods from Bashkiria*. Leningradskii Ordena Lenina Gosudarstvennyi Universitet, Leningrad, 63 p., 5 pls. (In Russian.)

MUIR-WOOD, H. M., 1965. Productidina. 1n *Treatise on Invertebrate Paleontology, part H—Brachiopoda*, R. C. Moore, cd., Geological Society of America and University of Kansas Press, Lawrence, p. H439–H521.

MUIR-WOOD, H. M. & COOPER, G. A., 1960. Morphology, classification and life habits of the Productoidea (Brachiopoda). *Geological Society of America, Memoir* 81, 447 p., 135 pls.

NAKAMURA, K., KIMURA, G. & WINSNES, T. S., 1987. Brachiopod zonation and age of thc Permian Kapp Starostin Formation (Central Spitsbergen). *Polar Research* 5, new ser.: 207–219.

NASSICHUK, W. W., 1971. Permian ammonoids and nautiloids, southeastern Eaglc Plain, Yukon Tcrritory. *Journal of Paleontology* 45(4): 1001–1021.

NELSON, S. J. & NELSON, E. R., 1985. Allocthonous Permian micro- and macro-fauna, Kamloops area, British Columbia. *Canadian Journal of Earth Sciences* 22(3): 442–451.

RUZHENCEV, V. E., 1952. Biostratigraphy of the Sakmarian Stage in Aktybinsk region of Kazkhstan. *Akademiia Nauk SSSR, Paleontologicheskii Institut, Trudy* 42, 90 p., 6 pls. (In Russian.)

SARYCHEVA, T. G., LIKHAREV, B. K. & SOKOLSKAYA,

A. N., 1960. Order Productida. In *Osnovy Paleontologii. Vol. 7. Mshanki Brachi* [Principles of Paleontology. Vol. 7. Phylum Brachiopoda], T. G. Sarytchcva, ed., Akademiia Nauk SSSR, Moscow, p. 221–238. (In Russian.)

SCOTESE, C. R. & McKERROW, W. S., 1990. Revised world maps and introduction. In Palaeozoic Palaeogeography and Biogeography, W. S. McKerrow & C. R. Scotesc, eds, *Geological Society of London, Memoir* 12: 1–21.

SHI, G. R., 1991. *Lower Permian brachiopods and molluscs from Tatonduk River Formation (new formation) of northern Yukon Territory, Canada.* Unpublished Ph.D. thesis, University of Queensland, Australia, 445 p., 32 pls.

SHI, G. R., 1994. The Late Palaeozoic brachiopod productid gcnus *Jakutoproductus* Kashirtsev 1959 and the *Jakutoproductus verchoyanicus* Zone, northern Yukon Territory, Canada. *Alcheringa* 18: 103–120.

SHI, G. R. & ARCHBOLD, N. W., 1995. A quantitative analysis on the distribution of Baigendzhinian-Early Kungurian (Early Permian) brachiopod faunas in the western Pacific region. *Journal of Southeast Asian Earth Sciences* (in press).

SHI, G. R., ARCHBOLD, N. W. & ZHAN, L.-P., 1995. Distribution and characteristics of mid-Permian (Late Artinskian-Ufimian) mixed (transitional) marine faunas in Asia and their palaeogeographical implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 114: 241–271.

SHI, G. R. & WATERHOUSE, J. B., 1991. Sakmarian (Early Permian) brachiopod biogeography and major gencric associations as rclated to terrane drift. In *Brachiopods Through Time*, D. I. MacKinnon, D. E. Lee & J. D. Campbell, eds, A. A. Balkema, Rotterdam, p. 355–365.

STANLEY, G. D., JR & YANCEY, T. E., 1990. Paleobiogeography of the ancient Pacific — Technical Comments. *Science* 249: 680–681.

STEHLI, F. G. & GRANT, R. E., 1971. Permian brachiopods from Axel Heiberg Island, Canada, and an index of sampling efficiency. *Journal of Paleontology* 45(3): 502–521.

STEPANOV, D. L., 1951. Upper Palaeozoic of the western slope of the Urals. *Trudy Vsesouznogo Neftianogo Nauchno-Issledovatel'skogo Geologo-Razvedochnogo Instituta (VNIGRI), new. ser.* 54: 1–221. (In Russian.)

STEVENS, C. H., 1985. Reconstruction of Pcrmian palaeogeography based on distribution of Tethyan faunal elements. In *Compte Rendu. Vol. 5. Paleontology, Paleoecology, Paleogeography*, J. T. Dutro, Jr & H. W. Pfefferkorn, eds, Southern Illinois University Press, Carbondale, p. 383–393.

STUCKENBERG, A., 1875. *Report on a geological journey to Pechora Land and the Timan Tundra. Materials for the Geology of Russia*, 6. Imp. Soc. St Petersburg Rept., 216 p.

TAZAWA, J.-I., 1987. Permian brachiopod faunas of Japan and their palacobiogeographical significance. *Gekkan Kagaku* 9(5): 252–255.

TAZAWA, J.-I., 1991. Middle Permian brachiopod biogeography of Japan and adjacent regions in East Asia. In *Pre-Jurassic Geology of Inner Mongolia*, K. Ishii, X. Liu, K. Ichikawa & B. Huang, eds, China. Matsuya Insatsu, Osaka, p. 213–230.

TOULA, F., 1875. *Perrno-Karbon fossilien von der Westk-ste von Spitsbergen. Neues Jahrbuch f-r Mineralogie und Palaontolgie*, p. 225–264, pls 5–10.

USTRITSKIY, V. I., 1961. Distribution of brachiopods in the Upper Palaeozoic Arctic zoogeographical rcgion. *Palaeontologichwskii Zhurnal* 1961(3): 3–13. (In Russian.)

USTRITSKIY, V. I., 1968. Position of the North Pole in the Late Palacozoic from the palacontological data. *International Geological Review* 9(10): 1268–1274.

USTRITSKIY, V. I., 1971. Biostratigraphy of the Upper Palaeozoic in the Arctic. *Nauchno-Issledovatel'skii Institut Geologii Arktiki (NIIGA), Trudy* 164, 279 p. (In Russian.)

USTRITSKIY, V. I. & CHERNYAK, G. E., 1963. Biostratigraphy and brachiopods of thc Upper Palaeozoic of Taimyr. *Nauchno-Issledovatel'skogo Institut Geologii Arktiki, Trudy* 134, 139 p., 47 pls. (In Russian.)

VOLGIN, V. I., 1960. *Brachiopoda of the Upper Carboniferous and Lower Permian Deposits of Southern Fergana.* Leningradskii Ordena Lenina Gosudarstvennyi Universtet, Leningrad, 202 p., 18 pls. (In Russian.)

WARDLAW, B. R., NESTELL, M. K. & DUTRO, J. T., JR, 1982. Biostratigraphy and structural setting of the Permian Coyote Butte Formation of central Oregon. *Geology* 10(1): 13–16.

WATERHOUSE, J. B., 1975. New Pcrmian and Triassic brachiopod taxa. *University of Queensland, Department of Geology Papers* 7(1), 23 p., 2 pls.

WATERHOUSE, J. B., 1978. Pcrmian Brachiopoda and Mollusca from north-west Nepal. *Palaeontolographica Abt. A* 160(1–6): 1–175.

WATERHOUSE, J. B. & PIYASIN, S., 1970. Mid-Permian brachiopods from Khao Phrik, Thailand. *Palaeontographica, Abt. A* 135(3–6): 83–197.

WATERHOUSE, J. B. & WADDINGTON, J., 1982. Systematic descriptions, palaeoecology and corrclations of the Late Palaeozoic subfamily Spiriferellinae (Brachiopoda) from the Yukon Territory and the Canadian Arctic Archipelago. *Geological Survey of Canada, Bulletin* 289, 72 p., 8 pls.

WIMAN, C., 1914. Uber die Karbonbrachiopodcn Spitsbergen und Beeren Eilands. *Nova Acta Reg. Soc. Sci. Upsaliensis, ser. IV* 3(8), 91 p.

YANCEY, T. E., 1975. Permian marine biotic provinces in North America. *Journal of Paleontology* 49: 758–766.

YOCHELSON, E. L., 1968. Biostratigraphy of the Phosphoria, Park City, and Shedhorn formations. *U.S. Geological Survey Professional Paper* 313-D: 571–657.

YOLE, R. W., 1963. An Early Permian fauna from Vancouver Island, British Columbia. *Bulletin of*

Canadian Petroleum Geology 11(2): 138–249.

ZAVODOVSKIY, V. M. & STEPANOV, D. L., 1971. Brachiopoda. In *Polevoi Atlas Permskoi Fauny i Flory Severo-vostoka SSSR* [Field Atlas of the Permian Fauna and Flora of the Northeast U.S.S.R.], M. V. Kulikov, ed., Severo-Vostoehnoe Ordena Trydovogo Krasnogo Znameni Geologieheskoe Upravlenie, Magadan, p. 70–182, 96 pls. (In Russian.)

ZHANG, C., ZHANG, F.-M., ZHANG, X.-G. & WANG, Z., 1983. Brachiopoda. In *Palaeontological Atlas of Northwest China. Xinjiang Volume. Pt 2. Upper Palaeozoic*. Geological Publishing House, Beijing, p. 282–386.

TRANSACTIONS

OF THE

ROYAL SOCIETY OF VICTORIA

THRYPTOMENE CALYCINA: ITS REPRODUCTIVE BIOLOGY AND ITS DEVELOPMENT AS A CUT FLOWER CROP*

DAVID BEARDSELL

Institute for Horticultural Development, Private Bag 15, South Eastern Mail Centre, Victoria 3176, Australia.

'On the steep slopes grew pines, *casuarinae*, and a variety of shrubs, among which we found a fine new species of *Baeckea*, forming a handsome evergreen bush, the ends of whose graceful branches were closely covered with small white delicate flowers.'

Major Thomas L. Mitchell, July 23, 1836

Thryptomene calycina (Lindl.) Stapf is one of approximately 35 species in a genus that is represented in most parts of Australia. It only occurs naturally in the Grampians (Gariwerd) and Black Ranges in western Victoria, and is locally known as Grampians thryptomene. This name is no longer relevant, and to promote it, especially overseas, it should be called 'Victorian laceflower'. This wonderful shrub was discovered by the early Australian explorer Major Thomas Mitchell (1839—see quotation above). It was described by J. C. Schauer (1843) as *Paryphantha mitchelliana*, although the first description was by Lindley in 1839 as *Baeckea calycina*. To add to the confusion, von Mueller (1858) transferred the species to Endlicher's genus *Thryptomene* as *T. mitchelliana*. Stapf (1924) correctly recombined the species as *T. calycina* since Lindley's description pre-dated Schauer's. Unfortunately, recent work (Beardsell 1991) shows that the current taxonomic ranking is inappropriate, and all eastern members of the genus *Thryptomene* should be placed into a separate genus. Further research is required, however eastern Australian members of *Thryptomene* would be placed into *Paryphantha*. This genus is however based on the illegitimate name *Paryphantha mitchelliana*, so that a new generic binomial may be required.

The following is a summary of the reproductive biology and horticulture of this Victorian endemic plant.

FLOWERING BEHAVIOUR

Thryptomene calycina flowers from May to October with hundreds of small flowers open at the one time for most of winter. Flower initiation commences in November under the influence of long days and higher temperatures and continues until April. The flowers open acropetally with the last flowers opening near the growing shoot tip in spring.

FLORAL SECRETIONS

Flowers of *Thryptomene calycina* contain two types of secretory tissue (Beardsell et al. 1989). Nectaries of the floral tube secrete a nectar rich in fructose and glucose through the numerous nectar secreting pores in the epidermis. Plants which have nectar low in sucrose, the common plant sugar, are rare (Gottsberger et al. 1984). The secretory cells are densely-packed and have few vascular connections. The five anther connectives each terminate in a gland, which at anthesis contains large, thin cells. The gland contains an hydrophobic material which stains positively for lipids and probably contains phenolics. This material is secreted through a pore at the end of the gland where it collects and mixes with pollen to form a food source for insects. This dual secretion of food materials should ensure that a wide range of pollinating insects visit the flowers (Beardsell et al. 1993a). This is the first assignment of a role for the anther glands which are found in most Australian Myrtaceae.

BREEDING SYSTEM AND REPRODUCTIVE EFFICIENCY

Thryptomene calycina is highly self-incompatible, with an Index of Self-Incompatibility of between 0 and 0.1 (Beardsell et al. 1993a). The site of arrest of self-incompatible pollen tubes is near the micropyle of the ovule, so that it is a late acting mechanism in this species. In wild populations,

---

1

the natural seed set varies between 9 and 13%. Pollination is not a factor limiting seed set in these flowers since every stigma examined from wild populations carried some germinated pollen grains. The low level of seed production is because most pollinations are probably ineffective selfs which occur when pollen exudes from pores in the anthers directly over the stigma; air currents and rain splashing probably accentuate the effect. Self-pollination is facilitated by the long period of stigma receptivity which occurs for 12 days commencing 2 days after anthesis and the long period of pollen viability (up to 15 days). Each flower contains approximately 60 000 pollen grains, and the pollen-ovule ratio is one of the highest so far found in plants, and is indicative of a strongly outcrossing breeding system. Most pollen is shed 3 days after anthesis, but this depends on temperature, relative humidity and probably the water potential of flowers. Despite the poor seed set, many seedlings develop under bushes after soil disturbance. The reproductive success must be due to the large numbers of flowers produced per bush per season, combined with the annual shedding of indehiscent nuts some of which contain dormant seeds.

INSECT POLLINATION

In winter, the only insects found on the flowers are flightless Thysanoptera which perform geitonogamous pollinations (Beardsell et al. 1993a). Towards the end of the flowering season immature and winged Thysanoptera and flies, bees and beetles visit flowers. Many small flies feed on the flowers but carry few pollen grains and are not pollinators. Some blow flies carry pollen, but the medium sized flies *Melagyne* sp. and *Duomyia* sp., and the bee, *Leioproctus* sp. are the main pollinators on the rare warm days of early spring.

SEED AND FRUIT DEVELOPMENT

At anthesis, the receptacle of flowers of *T. calycina* is enclosed by a layer of small cells with a thick cuticle. The hypodermis consists mostly of large oil-containing cells interspersed with much smaller cells. The tissue surrounding the ovary consists mostly of spongy parenchyma. The micropyle of the ovule is formed only by the inner integument which is double-layered. The embryo sac at anthesis is typical of the Myrtaceae, and appears to follow the monosporic polygonum type, with considerable nucellar tissue surrounding it. In a mature fruit the parenchyma is compressed into a thin band surrounding the seed (Beardsell et al. 1993b). The

integuments form a two-layered seed coat within the fruit. The aborted ovule is displaced below and to one side of the developing seed. In fruit weathered for several years, there is an accumulation of phenolic material giving the fruit a black appearance. The two layers of the seed coat within freshly shed fruit lie closely together and stain strongly with the lipid stain auramine O. In fruit weathered for at least 2 years, the two layers of the seed coat become separated for at least part of their length, and staining from auramine O is less intense. The breakdown in seed dormancy in weathered fruits is probably due to a less complete barrier to water uptake provided by the separation of the two layers. This would increase lateral and radial movement of water. The observed reduction in the hydrophobic lipid content of the testa layers probably also aids water entry into the seed in a weathered fruit.

SEED GERMINATION

Freshly fallen fruits of *T. calycina* contain seeds which are completely dormant; none germinate after 200 days at 20°C (Beardsell et al. 1993c). Seeds excised with testas intact from fresh fruits are partially dormant; one-third germinating after 60 days. The dormancy of seeds in freshly fallen fruits is imposed jointly by the fruit and the seed. The major site of the dormancy is the seed coat, since tearing part of it away from seeds excised from fresh fruits results in rapid and complete germination. Fruits stored dry in a laboratory at 20°C for 90 days are partially dormant. Nicking the distal end of these fruits enhances germination. Seeds excised from these laboratory stored fruits have 85% germination, which indicates a reduction in the seed imposed dormancy. Germination of *T. calycina* is independent of light and, although the fruits contain large amounts of phenolic material, this does not inhibit germination. Fruits weathered in the field for at least 2 years contain less viable seeds, presumably because of insect predation, but these all germinate within 50 days at 20°C. Brief washing of fruits in concentrated sulphuric acid increases germination. Germination is not enhanced by treatment with low concentrations of gibberellic acid in the presence or absence of cytokinin.

MICROSPOROGENESIS

The chromosomes of *T. calycina*, like most Myrtaceae, are very small and difficult to resolve clearly using bright field or Nomarski differential interference microscopy. A superior protocol for
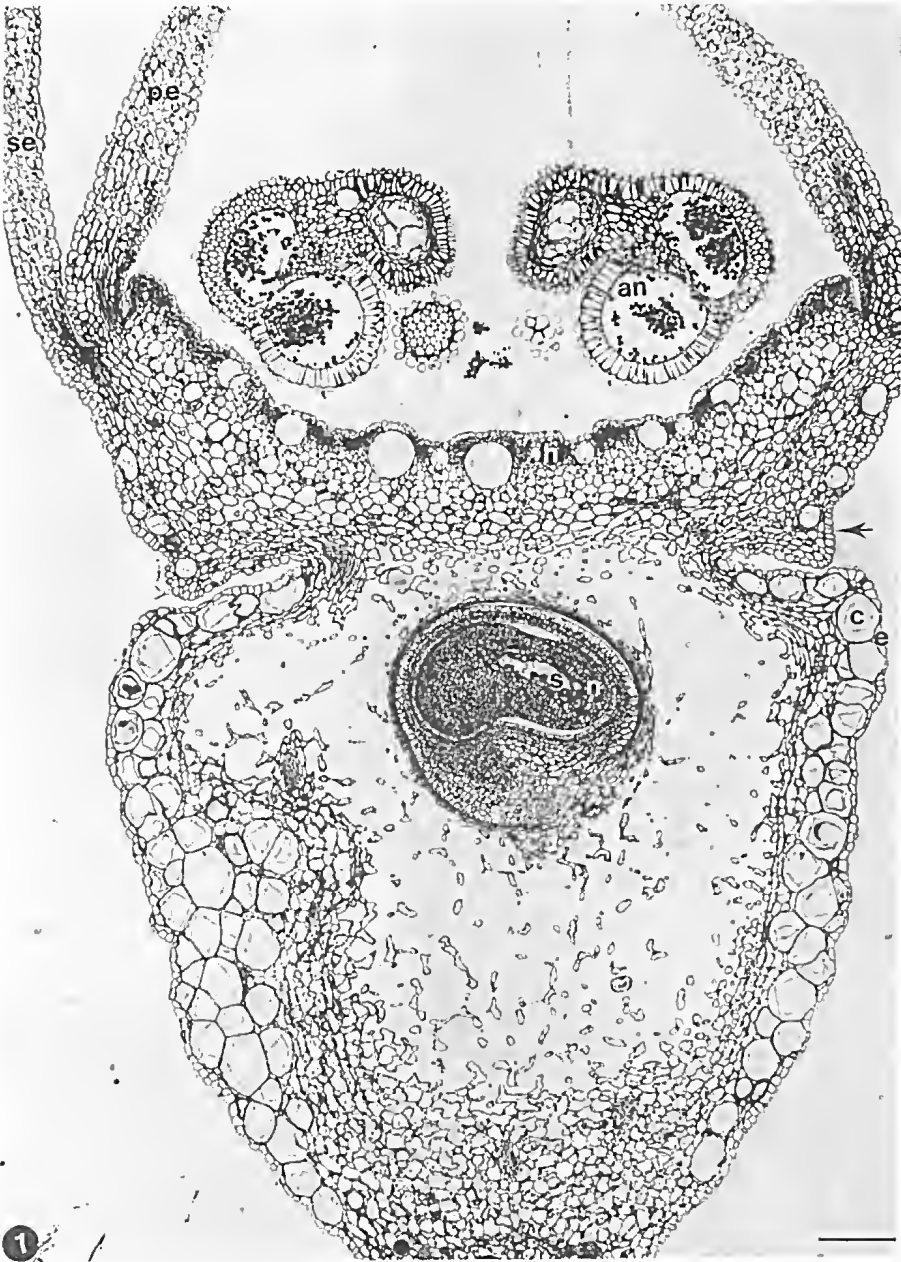
Fig. 1. A longitudinal section stained with toluidine blue O of a flower of *T. calycina* at anthesis, showing the ovary and receptacle structure. A thick cuticle (arrowed) and thick walled epidermal cells (e) enclose the receptacle including the hypanthium nectary (h). The hypodermis consists mostly of oil cells (c). The nucellus (n) and the embryo sac (s) of the ovule are shown. The sepals (se), petals (pe) and anthers (an) are also shown. Scale: 150 μm.
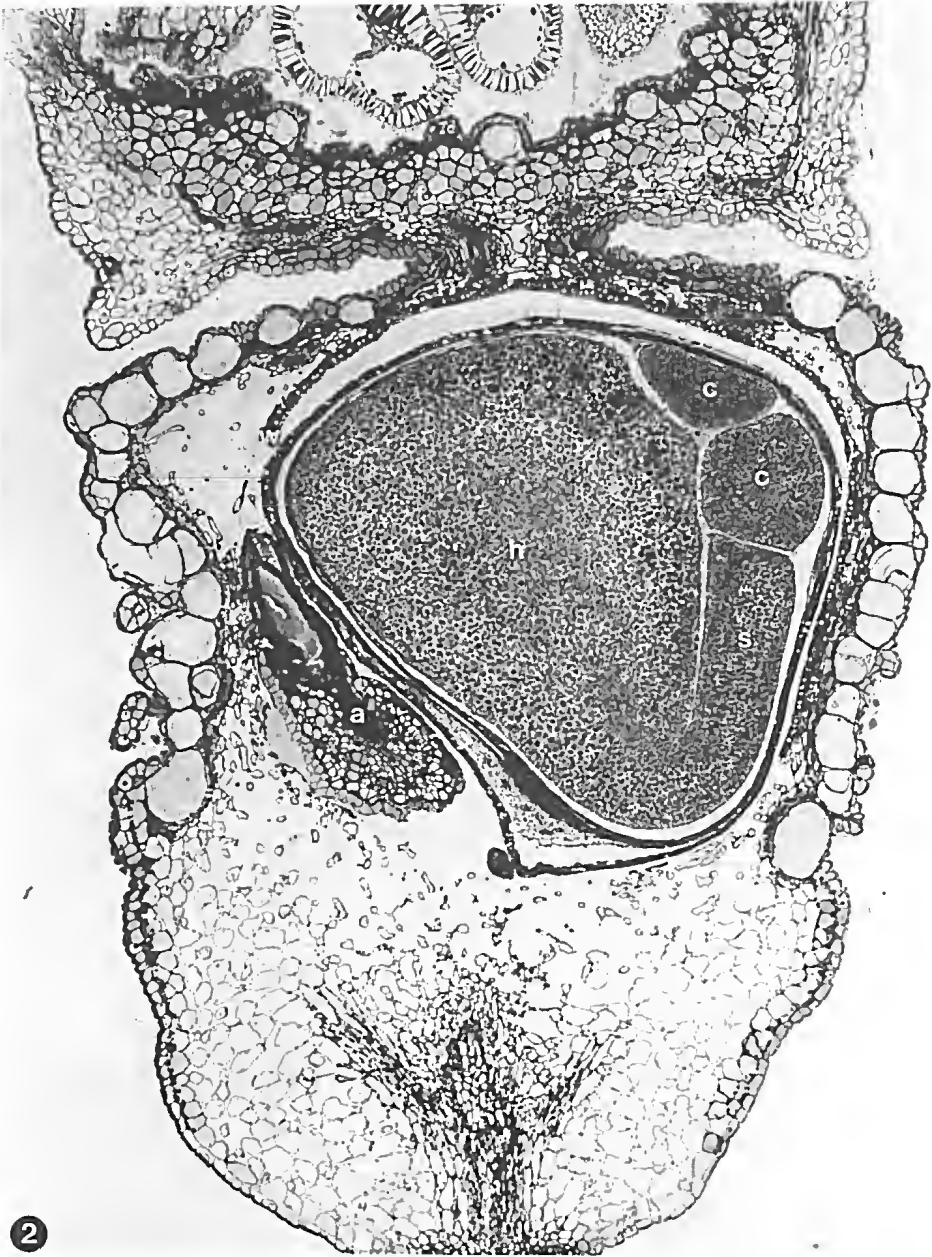
Fig. 2. Longitudinal section stained with toluidine blue O of a freshly shed fruit. The aborted second ovule (a) is displaced below and to the side of the seed. The seed consists mainly of hypocotyl tissue (h), the cells of which contain starch and/or lipid bodies. The cotyledons (c) have a long stalk (s). The developed seed has ruptured the ovary wall (w) and compressed the surrounding spongy parenchyma. The senescent hypanthium (f) remains attached. Scale: 140 μm.

resolving these small chromosomes during male germ cell development using the DNA specific probes DAPI and Hoechst 33258 (Beardsell et al. 1990) was developed. The method requires a fixative containing chloroform to remove auto-fluorescent lipids from the anther gland, a pre-treatment with acetic acid and a pH of at least 6 during treatment with DNA probes. This method should become the standard for examination of microsporogenesis and for determination of haploid chromosome numbers in plants. The fine threads of the chromosome bivalents are readily seen during pachytene and diakinesis. The paired chromosomes are extremely well resolved during metaphase I. The haploid number of *T. calycina* is 11, and meiosis is similar to other Myrtaceae. Natural tetraploids occur. Mitosis in the pollen grain was also well resolved, and two unequal nuclei were formed; the putative generative nucleus being elongated and densely staining.

MUTANT FLOWERS

Twenty plants with various phenotypic abnormalities to the flowers were selected from very large populations of *Thryptomene calycina* in the Grampians and Black Ranges (Beardsell et al. 1993d). Most of these had impaired reproductive function. Normal flowers were epigynous with five sepals, five petals, five anthers, a single style and two anatropous ovules. The mutants were two partially male sterile, tetraploid plants with large flowers, one of which occasionally produced additional flowers from the leaf axils with peduncles as well as pedicels; one plant which produced a proportion of hexapetaloid flowers with six stamens; three gross mutants with fleshy, bracteoid pointed petals and sepals, no stamens, vestigial styles and stigmas, exposed ovules and no inferior ovary; one plant with fleshy, bracteoid pointed sepals, vestigial style and stigma but with the exposed ovular structures replaced by 4–5 sterile ovules generally inside an abnormal ovary; two plants with reduced ovary diameter and sterile ovules, shortened style, five reduced sepals and petals and 5–8 anthers; three anthocyanin-free plants; three plants with pink sepals; two plants with half-sized flowers which produced a proportion of fasciated stems; one plant which occasionally produced flowers without pedicels which virtually resulted in organs which were leaf-flower composites; two plants which produced sepals and petals which contained chlorophyll and prematurely senesced, and had partial substitution of petals by anthers. The structure of several of these mutants disproved some aspects of the modern theories on floral development.

HORTICULTURAL DEVELOPMENT

Thryptomene calycina is an important winter cut flower crop in Victoria, and export is increasing interstate and overseas. The farmgate value of the crop is worth over one million dollars, and this is increasing at approximately 15% per year. It is also grown as a cut flower crop in California, although the varieties there are of poor quality. A small industry operated by the Winfield and Edwards families living near its natural range has produced flowering stems for the winter flower markets in Australia since the 1930s, and several new plantations have been set up in recent years. Harvesting is usually done with secateurs and stems are tied into bunches of ten for storage and transport. Limited post-harvest handling treatments are used, but the flowering stems have a shelf life of up to 10 days if the stems are quickly placed in a cool store in buckets containing a flower preserving solution or covered with moistened cloth or hessian covers. Stems should be marketed within 24 hours of harvest. In Victoria, *T. calycina* is used in a similar role to gypsophila and *Limonium* species in the preparation of mixed bunches and it greatly compliments red or pink roses. It is however quite different in appearance to gypsophila. *Thryptomene* calycina has flowering branches which are coarser than the terminally flowered gypsophila species.

Dry weather in summer and autumn may cause leaf and flower bud drop, reducing the quality of flowering stems at harvest time. The first flowers open in May in most years, and flowering continues until early spring. Late and early varieties will extend this flowering season, and flower farms should grow a number of clonal (vegetatively propagated) selections which have different peak flowering times. This would enable high quality flowering stems (flowering stems with more than 50% of flowers open) to be harvested from field plantations throughout winter. Peak flowering is in July and August, and most plants should not be harvested later than the end of August because the quality, especially after harvesting, transport and storage, deteriorates rapidly after this time. This deterioration is due to two factors. Firstly, spring growth extends at the tips of branches which detracts from the overall appearance and reduces vase life of cut stems. Some clones produce greater stem extension than others, and the growth

is enhanced by fertilisers containing excessive nitrogen and by higher rainfall. Secondly, the abscission layer which allows the annual shedding of fruits in nature, starts to develop on older flowers lower down on the stems from August onwards. This leads to increasing flower drop as the season progresses, especially if significant cross-pollination of flowers by insects has occurred because of sunny weather in May–July. This is because fruits with developing seeds mature more quickly than unfertilised fruits. Flower farms which have large blocks of single cultivars will have less cross-pollination (which is essential for seed production in *T. calycina*) and possibly less premature fruit drop. Botrytis infection can also cause premature flower drop.

A number of pests and diseases have been found on *T. calycina*. Several species of thrips feed on the nectar and pollen produced by the flowers, webbing caterpillars feed on the foliage and borers can ring-bark stems. *Thrips* species need to be controlled on stems to be exported. This can be achieved by dipping of cut stems in an insecticide.

One of the main limitations is sensitivity to the root rotting pathogen *Phytophthora cinnamomi*. This has prevented it from becoming a well known landscape plant. *Thryptomene calycina* can however be readily grafted onto the more adaptable *T. saxicola* (Meyers 1993: Beardsell 1993), although this method of propagation has not yet been commercialised. Tip die-back of branches also occurs from an interaction of the pathogens *Botrytis* sp., *Pestalotiopsis* sp. and *Phoma* sp. This can be controlled by application of Mancozeb[R]. Flowering stems can also be damaged by severe frosts (below −3° Celsius).

The industry has been based on seedling stock; no cultivars have been available until recently. This has resulted in variability in flower quality. Because of the lack of available cultivars, a selection and breeding program was started in 1983 at the Institute of Plant Sciences (now Institute for Horticultural Development), Knoxfield. The aim was to develop a series of cultivars which had very dense flowering, a range of flowering times and long vase lives. In addition, mutant plants and selections which had pink flowers and white flowers were selected. Two outstanding massed flowering cultivars, 'Ivory Lace' and 'Coral Lace' have been released to industry.

All growers should also select the best seedlings from their plantations and have them commercially propagated by a tubestock nursery which has strict hygiene (to reduce chances of spreading *Phytophthora cinnamomi*). Victorian laceflower has the potential to be a world class flower like the new limoniums from Japan. It will not achieve this status however unless growers use only elite cultivars, some irrigation is applied in dry seasons (to prevent bud and leaf drop), flowers are marketed as soon as possible and are cool stored at 1 °C, and harvesting of poor quality stems (with shoot tip extension and flower drop) is not done in early spring. During the last three years the major growers have adopted most of these improved practices, and the main tasks not yet completed are the setting up of quality assurance and continuous improvement programs, and better market promotion. Growers also need to address losses caused by the root rotting pathogen, *Phytophthora cinnamomi*.

There are a number of other species of *Thryptomene* native to eastern Australia which could be developed as cut flowers if funding was made available. Those with the best potential are *T. ericae*, *T. elliotti*, *T. hexandra* and *T. parvifolia*. Since these are all closely related to *T. calycina*, they should not be planted near the Grampians or Black Ranges, otherwise they could cause genetic pollution.

REFERENCES

BEARDSELL, D. V., 1991. Reproductive biology of *Thryptomene calycina* (Lindl.) Stapf. PhD thesis, School of Botany, University of Melbourne.

BEARDSELL, D. V., 1993. Horticultural development of *Thryptomene calycina*. *Australian Plants* 17: 166–171.

BEARDSELL, D. V., WILLIAMS, E. G. & KNOX, R. B., 1989. The structure and histochemistry of the secretory tissue of the flowers of *Thryptomene calycina* (Lindl.) Stapf. *Australian Journal of Botany* 37: 65–80.

BEARDSELL, D. V., KNOX, R. B. & WILLIAMS, E. G., 1990. Use of DNA fluorochromes for studying meiosis in the woody species *Thryptomene calycina*. *Stain Technology* 65: 189–195.

BEARDSELL, D. V., WILLIAMS, E. G. & KNOX, R. B., 1993a. Breeding system and reproductive success in *Thryptomene calycina* (Myrtaceae). *Australian Journal of Botany* 41: 333–353.

BEARDSELL, D. V., KNOX, R. B. & WILLIAMS, E. G., 1993b. Fruit and seed structure of *Thryptomene calycina* (Myrtaceae). *Australian Journal of Botany* 41: 183–193.

BEARDSELL, D. V., WILLIAMS, E. G. & KNOX, R. B., 1993c. Germination of seeds from the fruits of *Thryptomene calycina* (Myrtaceae). *Australian Journal of Botany* 41: 263–273.

BEARDSELL, D. V., WILLIAMS, E. G. & KNOX, R. B., 1993d. Homeotic, Meristic and Cytological Floral Mutants of *Thryptomene calycina* (Lindl.) Stapf (family Myrtaceae). *Annals of Botany* 72: 27–36.

GOTTSBERGER, G., SCHRAUWEN, J. & LISKENS, H. F., 1984. Amino acids and sugars in nectar, and their putative evolutionary significance. *Plant Systematics and Evolution* 145: 55–77.

MEYERS, D. M., 1993. The grafting of Grampians thryptomene. *Australian Plants* 17: 78.

MITCHELL, T. L., 1839. 'Three Expeditions into the Interior of Eastern Australia.' Vol. 11. T. and W. Boone, London.

SCHAUER, J. C., 1843. *Linnaea* 17: 236.

STAPF, O., 1924. *Thryptomene thymifolia*. *Curtis's Botanical Magazine* 149, sub t. 8995.

VON MUELLER, F. J. H. 1858. *Fragmenta Phytographiae Australiae* 1: 11.

Dr Grisha A. Sklovsky, AM, FRACI
(1915–1995)

Dr Grigorig Abramovitch Sklovsky, a former President of the Royal Society of Victoria, died suddenly on 9 January 1995. In view of his many contributions to the nation, and particularly to Victorian science and technology, the Council of the Society has arranged for the publication of the following tributes which were paid to Dr Sklovsky at a Memorial Service held on 18 January 1995, at the Parkview Room, Camberwell Civic Centre, Camberwell, Victoria 3124.

WILL DARVALL   Welcome to the celebration of the spectacular life of Grisha Sklovsky.

I practised as Grisha's nephew from the time he arrived in Australia until his death and I practised as his doctor for twenty-five years. We shared many serious times, many intimacies and many jokes, and most of you can say exactly the same thing—because that was the incredible nature of the man, that he was interested in you, he was interested in what you thought and what you were doing and he was always humorous. The word 'life' became a quantitative word when it applied to Grisha, because who could have contributed more to family, friends, education, information industry and community than Grisha. Grigorig Abramovitch Sklovsky was born on the 6th October 1915 and died on the 9th January 1995, quietly and peacefully and unexpectedly in his sleep in his eightieth year. Today we have ten speakers.

BARBARA DARVALL (sister-in-law)   I keep on reminding myself that I am among friends because I wouldn't have taken up public speaking at 83 if I wasn't the only person, probably, who knows what happened during the War when Celia and Grisha showed their extraordinary positive thinking and knew exactly what they wanted. I first heard of Grisha in 1938 when Celia wrote to me from Lyon, where she was an au paire and Grisha was doing his doctorate. She spoke of him frequently in her letters until my family began to get a little anxious, because they were so afraid that she might decide to stay there, as they had fallen in love. Grisha wanted to marry her then and there. My mother was quite ill and likely to die at any time, and they were both anxious, so Celia decided to come home and get them all around to it and Grisha was to follow shortly. Well, in the meantime, Grisha took her to meet his mother and it was very salutary to us anxious Australians to hear that Grisha's mother was a bit horrified at him taking up with anyone from such an uncivilised country (we do realise what a lot Grisha did to civilise it). Anyway, she came back and the war broke out. She was getting letters and then of course she couldn't go and then there was the fall of France and Grisha disappeared and my dad, who had been very anxious, began to get very tolerant and when I congratulated him he said 'Well I think there's practically no chance we'll ever see the poor chap, I might as well be decent about it'. After a while a letter came: Grisha had done some miraculous escape,

wriggling out through Spain. Then the letters came and Grisha was brought to England and joined the Czech legion, where he had to live under canvas for years. We were very struck when a letter came saying how wonderful it was he'd been asked out and he'd actually sat in a room for an evening. Meanwhile, Celia was working as an Orthoptist with Dr Ringland Anderson (whose grandson has just recently saved Grisha's sight last year). During that time Celia had a bad motor accident and by some telepathy Grisha wrote and said he had a feeling that she was ill and sent her a most comforting letter. When the war finally ended, we were very worried about Grisha again during the invasion, but comforted by the fact that his eyesight would prevent him from being in the front line. Finally, when the war in Europe ended, the Japanese war was still going on and Celia couldn't get to Europe and Grisha couldn't get out and Celia discovered the only way to get nearer was to join the Australian Red Cross to work in Greece, so she did the training course and went. Grisha said he'd try to get there. She had been there for several months and one night as she was filling her hottie, as she had a bad cold, she was told that there was a young man she might be interested in meeting and in came Grisha. After that they got married twice because no-one knew who had jurisdiction. However, it must have worked, as Celia lost her nationality and they had three children so they must have been properly married. They stayed in Europe for another couple of months trying to trace Grisha's mother, who had disappeared in Paris the night they heard all the Gestapo cars roaring along the street, and there were agonising rumours from people who thought they had seen her, though he was never able to find out anything. In the meantime, when we found they were definitely coming back to Australia, my husband had been doing all the legal work, trying to pull any strings to make it easier for them to get back. When they arrived they stayed with us and we all talked to him at once. He did look staggeringly foreign to us dreadfully insular Australians and his accent was so thick but he was so matey. I had four small children at that stage; he just fitted in to the muddled household and the children loved him and he was so helpful. In no time we were able to tease him when he said 'Are you thinkink of ridink this mornink?'

I was told I must tell this silly story. My husband was extremely tired, as he had been overworking for a good many years and we were

due to go on a camping trip. So after they had stayed with us for a few weeks I realised that Grisha's gratitude was leading him to be so vital, so matey and so entertaining to my poor tired husband till late at night that Pip was getting rather glad to get away. They looked after the house, as their flat wasn't ready. When we got back everything was beautifully clean and tidy — much better than I would have had it; however Pip began saying that 'Everything smells of garlic'. He had a very sensitive and a nervous digestion and he got quite horribly Australian saying 'bloody foreigners, bloody garlic!'. So I began to clean everything more and more and everything got worse and worse. Finally I found a large sliver of garlic stuck in the soap saver. I was told I must tell that story.

I think that everyone knows that my children and grandchildren absolutely adored him. Some of the grandchildren burst into tears when they heard that he had died. His interest in my children was absolutely amazing. At their sensitive years they weren't always pleased to be told 'I've been talking to your professor about you', but, as they got older, they appreciated his incredible good will and wisdom and he helped them in many ways, one most especially. Actually, Shakespeare puts things much better that I do; 'His life was gentle and the elements so mixed in him that Nature might stand up and say to all the world this was a man'.

WILL DARVALL Our next speaker is Sam Moshinsky who also has known Grisha for many, many years. Grisha helped to bring his family out in 1951.

SAM MOSHINSKY I've been asked by Celia to provide you with a picture and a snapshot of Grisha's family background and early life in Siberia and Germany. Our family's connection, that is the Moshinsky's relationship to the Sklovskys, goes back a long way. My mother's grandfather and Grisha's grandmother were brother and sister. Their family name was Aptoman. Grisha's father and our maternal grandmother were cousins. Just to set the scene, the earliest record of the Sklovsky family is at the end of the 19th Century, and even then the Aptomans and the Sklovskys, like millions of Russian Jews, lived a very miserable existence under the yoke of an anti-Semitic Czarist regime. Not only were the means by which they could earn their livelihoods circumscribed by restrictive laws, they were also restricted to where they could live. As the suffocation of their persecution grew, the Jews sought to escape through emigration, which they did in large numbers. Most went West to the United States and England and also to Palestine to establish a Jewish state. However, a small number of Russian Jews were drawn to the East. Siberia was being economically opened up by the recent completion of the Trans-Siberian railway and the restrictions against the Jews there were less harsh on the theory, that the further you got away from the Czar in Moscow the better. The Sklovsky clan, then living in Gluchov, opted for the East and left for there at the turn of the century. Grisha's father joined his family there in 1903 upon completion of his studies. He was a born entrepreneur and became an extremely successful businessman right up to 1922, when the reach of the new Communist regime consolidated its position everywhere and began to put paid to all forms of private business activity. He was not only extremely able, but quick witted, a trait which Grisha inherited. Grisha recounts the following anecdote. In his early years of business expansion, Grisha's father wanted to establish a base in Chita, an important economic centre in Siberia, but it was still forbidden for Jews to live there. Not easily deterred, he tried a ruse by which to rent a room in a house there on the pretext of being a student. The landlady bought his story. However, during the initial interview in her parlour, she had to excuse herself and suggested to Grisha's father that he leaf through the photo album. In doing so, he noticed a face that he recognised as the local police chief, on whose list he knew he was. When the landlady returned, she noticed him looking at the photo and said 'Oh this is my favourite cousin, you'll like him, he comes here often.'. Grisha's father kept his cool, he did not bolt. He booked the room and later rang to cancel, explaining that he had been called away. In 1912 Grisha's father married his mother, a distant cousin, who was studying in Kiev. They married soon after she completed her medical studies. He then brought her to Stretensk, also in eastern Siberia, where the family was then based, and three years later Grisha was born. He would have been eighty years young in October of this year. Just before his 7th birthday Grisha recalls being called into his mother's room and shown his sister, Sofie. His notes record the following 'I loved her immediately and was the first ever to kiss her'. The Sklovsky's lived a very comfortable but active life. His father was away a lot on business, travelling up and down the Trans-Siberian rail-

way and from him Grisha inherited another attribute, helping others. His father helped a lot of people and even established a number of hospitals in nearby towns just so that his wife could maintain her medical skills. Grisha's ebullient personality came to the fore early in his childhood. He was very popular with his friends. So much so that his father once said that he had overheard Grisha's young friends say to each other, when the father entered his house, 'Oh that's the chap that is staying with Grisha'. Grisha and Sofie were blessed with wonderful parents, they were warm and frank about all things and they were determined to expose them, which they did, to a variety of cultures and a very, very liberal outlook. In 1925 when the business of Siberia wound down, the family moved to Berlin and they installed themselves in a comfortable neighbourhood. They arrived at a point of time when the then Weimar Republic was on the threshold of what was to be a great, but unfortunately, brief period of culture and freedom—for before long the dark clouds of Nazism started to appear. Grisha's first school in Berlin was a total disaster. During his first days, being new to Germany, he made an inordinately large number of mistakes in a dictation test. His teacher insisted upon administering a caning. Grisha remonstrated, saying that he could understand such punishment for matters of discipline and behaviour but not for genuine ignorance. When the teacher still would not relent, he simply got up and walked out. Despite his mother's pleadings, Grisha refused to return to the school, stating that his sense of justice would not permit him to do so. He quotes in his notes, 'This sense of justice has been a guiding principle in my life and strongly affected my attitude and decisions in all matters'. Time does not permit a more detailed account of the rest of his schooling in Berlin, where he matriculated, except to say that his next school and teachers were chosen with greater care. These were also years where he developed lifelong friendships, like Walter Juder, the Hertzenbergs and the Vialkovs, with whom he corresponded right up to the end. Grisha's father in Berlin had established a successful timber business, based in Poland, but unfortunately died suddenly in 1934 in Warsaw. His mother survived him for a number of years but, as you have heard, she perished in the Holocaust. His sister Sofie died of cancer last year in Paris. Grisha witnessed the rise of Nazism and its devastating anti-Semitism. He saw for himself the book burnings and the excesses of the storm troopers. His upbringing and experiences moulded him as a person and as a Jew. He was proud of his heritage but rejected its religiosity. He believed in integration and therefore was totally comfortable with marrying Celia and the way they brought up Anna, Michael and Janey, of whom he was so proud. But he also states in his notes that he supported the creation of the State of Israel and even admits some regrets in not being involved personally in the drama of its establishment and development. He was indeed a citizen of this world. I will leave it to others, as you have heard from Barbara, to elaborate on his later life, the move to Paris, the studies at Lyon University, where he obtained a doctorate in chemistry, his wartime army service, his marriage to Celia, and his establishment of a new and successful life full of achievement in Australia. In conclusion I would appreciate your indulgence for a few more minutes for what I feel I must recount and place for the record: a critical role in rescuing my family from Shanghai and bringing us to Melbourne. When the Chinese communists took over in 1949, my family, too, had to abandon their commercial interests in Shanghai. We were pressured to leave China but we were stateless and had nowhere to go. My mother, who like Grisha always writes to everybody and knows where everybody is, managed to obtain from an uncle of Grisha's, still living in Harbin in Manchuria, Grisha's address in Melbourne and wrote to him describing our family's plight. What we needed was for an Australian to sponsor us and to assure the Australian government that we would not be a charge upon it, upon arrival here. Grisha responded immediately and warmly and in 1951 the necessary papers were issued. It should be born in mind that all this correspondence took place in the early 1950s with the Korean war at full height, with China on one side and Australia on the other side and certainly correspondence was slow, tortuous and difficult, but it certainly took place. Then my family decided to send me at the age of seventeen to Australia on my own. Could the Sklovskys accommodate me until the rest of the family arrived. He realised that it was a great ask but the answer was again in the ready affirmative and for this I must thank Celia, specifically, for her ready concurrence as well, for I imagine by now she must have started to wonder what she was getting herself into with Grisha and his Russian relatives, whom she had never even met. My arrival in Melbourne

on Cup Day in 1951 did not spell the end of Grisha's involvement, although he and Celia had already done so much. He took one look at me and realised that he was facing a major challenge. For quite obviously my semi-Colonial upbringing in Shanghai had rendered me totally unsuitable for life in Australia. He taught me how to wield a broom, how to hand mow a lawn, to wash the dishes and to even take out the rubbish on a Sunday night. He even sent me on a 1500-mile hitch-hiking trip around Australia to get to know the country. He guided me in my studies and my career. He was a true mentor. He was not only a gifted man but a great giver as well. Our family today not only celebrates a life of achievement, we also mourn his untimely passing.

WILL DARVALL Kate Blaubaum (Kate Red-wood) the surrogate daughter from the years when surrogacy was not fraught with all the legal problems of today.

KATE BLAUBAUM This is a special opportunity for me to express my thanks to the Sklovsky family, in particular Grisha and Celia, for the way in which, with enormous warm hearted-ness and endless generosity, they have included me in their noisy, energetic, argumentative, positive, opinionated, caring, chaotic, creative, humorous and loving family. Given half a chance I suspect that there would be a large contingent up here beside me to give a rousing thank you for such inclusion and a big cheer for Celia and Grisha. As some of you would know, I've spent quite a lot of time involved with the develop-ment of social policy and, in the last year, have given considerable thought to the issue of the year 'The International Year of the Family' which has involved the deliberation of many bureaucrats and academics who, I think, have totally forgotten to recognise a new family type. The new international elastic family — the Sklovsky family. This elastic family, which welcomed in over the years waifs and strays, refugees and visitors, friends and relations, was based on a wonderful partnership. Grisha full of energy, expansiveness, warmth, ideas and opinions. Celia, providing not only what we these days refer to as the infrastructure but the practical loving care. In the 39 years that I knew Grisha, what struck me very forcibly was the diversity of people who were drawn into Grisha's ambit and in whom he invested time and effort. The diverse kinds of assistance which he provided for them and the long term commit-

ment. Few people maintain friendships and associations with so many people over such a lengthy period of time as Grisha. Speaking for myself, Grisha and Celia took me on as a solemn and most unprepossessing six-year-old. They treated me as one of their own kids, and I can't comment on the results but I can only say that it felt good at the time. I remember in particular the annual convoy to Apollo Bay with the rituals of camping on Wild Dog Creek. 'Good God who left the ice box door open.' The catching of eels and Grisha skinning them with the pliers. The tennis on the Watkins' tennis court and the large gatherings at night and on the beach. As we grew older, Grisha's concern regarding our educational progress. The debates and arguments on issues of public concern. 'Good God you're older than I am' he'd say to us, a frequent comment to the young. Grisha providing me with my first experience of employment as a vacation student at ICI in the pre-car radio days, when we'd drive from Camberwell to Ascot Vale with the transistor radio in order not to miss the news and not to miss the share market report. Grisha providing me with a reference to get my first real job in England — it must have been a good reference to get a job from Australia. Grisha as speech maker on special occasions and I remember in particular the impromptu speech that he gave at Ron's and my wedding. Grisha's encouragement of membership in important bodies and associations as a means of developing the careers of us young adults with varying success and his particular habit of keeping copies of special papers and reports that we all must read. And more recently, Grisha as mentor and political adviser, early in the morning, 'I heard you on the radio this morning, can I give you a little advice', and you knew that any media appearance would not go unnoticed. Grisha larger than life, boundlessly generous of ideas, energy and resources. Grisha, we'll miss you dreadfully. However, the international elastic family lives on, and Grisha, what was the joke about the wheelbarrow that went ping, ping? I hope someone remembers.

WILL DARVALL Hans Snellerman, who shared a 40-year friendship and who is also from Europe.

HANS SNELLERMAN It's a great privilege to be able to say a few things about Grisha. A friendship of over 40 years. I'm also a new-comer — I don't come from Shanghai, I come

from Holland. Grisha and I and our families of course have shared many wonderful times in this period. Our association was particularly in sport. I think we all know that Grisha was not particularly keen on sport, he was a man of intellect, brains, thoughts, and the physical side of life — work in the garden and things like that — had very low priority. I remember him saying that his major contribution to work around the house was signing cheques. I hadn't heard him say much about sport and things like that although he did say he was a member of the Boy Scouts in Berlin in the late 1920s. Of course there was the Army, and there was skiing, and there was tennis. And in the skiing we used to go up in my car, which he rather critically referred to as that cheap German car — you know what car it was. But he relented and of course it always gave wonderful opportunities for those in the car — you were a captive audience — to discuss and to argue and to also talk to the children. My children too. His ability, his sense of fun of course, his jokes, we know them all, they still go around, about Elvis the Pelvis who had a brother[?]. His real interest in their problems is something that will stay with us always. On the tennis court he was, as Grisha always was, very clever. He was not a great player but he was quite strong at the net and he developed a little practice when you did something really clever (and I should remind you that I am the youngest member of our tennis club and we call ourselves the geriatric tennis club), but when somebody did something very good he'd say 'Pardon' like the French do and Grisha could do that with a wonderful varying degree of sincerity. If he really had tricked somebody he'd say 'Pardon' — that had become a standard pattern with us over the years. Quite some time ago Grisha had a double hip replacement and not so long ago he had major eye surgery. Never mind the hip replacement, he came back to the court and hit the ball as well as he could and the only concession after the eye operation was that he preferred to serve from the forehand court side because it was better for his eyesight. We shared wonderful times for which we and our family are very, very grateful. In thinking about him I could only quote the words of a hymn of thanksgiving 'Now thank we all our God, with heart, with hands, with voices, Who wondrous things has done, In whom His world rejoices'. I suggest that Grisha was one of these wondrous things in our life and that for the rest of our lives we will always rejoice in having known him.

WILL DARVALL Listening to Hans reminds me of one of Grisha's famous statements 'Any bloody fool can work; it takes brains to organise'. Our next speaker is Gus Nossal, long time friend and fellow refugee.

GUS NOSSAL Sklovskys all, dear colleagues and friends. My role in today's adventure is to attest to Grisha's high professional competence and to his unfailing support of research, development, innovation and progress. The context of my first professional contact with Grisha, over 35 years ago, is absolutely typical. It was when a close friend of mine, a prominent plant scientist, had just returned from Cambridge and was getting going at the Central Research Labs of ICI and, of course, who immediately became his mentor, his guide, his friend, but Grisha. That was how I saw Grisha and his work at ICI. The person was Martin Canny, as many of you will know, who had some excellent years at ICI and then went on to become the foundation professor of botany at Monash University and had a very distinguished scientific career.

Grisha was amongst the first people to realise that library science was about much more than books and journals. He was really amongst the very first to realise the huge impact that computers would have on the field. He was the first to realise that information technology was a separate, pristine science in its own right. He was extremely prominent in forging government policy in the '60s and '70s as this field took off. There was of course the famous Science and Technology Information Report, the so called STISEC report, which set the pattern for government policy in information technology especially interlibrary cooperation and the access of Australian libraries to the international databases which today of course we all take for granted. I had my second reasonably close professional contact with Grisha for three brief years during which the late Ken Myer asked me to join the National Library Council and the reason was that the National Library was getting much more interested in science and technology and indeed founded the National Science Library as part of the Library in Canberra. It didn't take long for Grisha to brief me on the fact that there was a certain rivalry between CSIRO, the NLA (National Library of Australia) and the Association of University Libraries as to who really had the primacy in information technology, and Grisha typically bent every energy on various committees and bodies and sub-

committees to ensure that somehow all of these forces worked together. Indeed that did happen and I'm happy to say that the situation at the present day between these major science libraries of the nation is very collegial indeed. If there have been any regrets, one of my great ones is that I never had the chance to talk to Grisha about the information super highway. I think I know what he would have said and my opinion on that is shaped by my third substantive professional contact with Grisha, when I asked him to do a brief but quite important consultancy, after his retirement, on the information systems within the Walter and Eliza Hall Institute. I can guess what Grisha might have thought about the information super highway. He would not have been overly concerned about the details of optical fibres in the network. He would not have spent a lot of time thinking about the computer hardware behind it. But he would have been very concerned about systems design and, above all, about the material that was to be transmitted, about the vehicles on the super highway. He was one for the strategic elements, the ideas behind a venture. The 'Big Picture'. This rich professional life, both before and after retirement from ICI, was honoured by the award of the Order of Australia to Grisha and he certainly would have been among the earlier non-Australian-born recipients of our National honour. This Australian honour our citizen of the world rightly and justly treasured.

May I close with just a couple of more personal reflections. What a partnership between Grisha, the man of science, the man of accuracy, the technical supremo in a most important but highly specialised field, and Celia, the painter, the creator of wonderful gardens, the artistic spirit whose high humanities-oriented intelligence we all admire so much. A truly wondrous complementation. Finally, whence came Grisha's rugged and courageous individualism? Over twenty years ago, Grisha and Celia visited Lyn and me while we were temporarily living in Paris and there were chances for some in depth conversations, perhaps somewhat longer conversations than in the normal Australian hurly burly, and it was here that we learnt some of the early experiences that we have been talking about earlier today which lead Grisha into a deep hatred of repressive regimes and terror-based curtailment of civil liberties. This freedom of the human spirit meant more to Grisha than almost anything else. Who among us has not benefited from this characteristic of our huge hearted, unquenchably positive and generous friend?

WILL DARVALL Mention of the Order of Australia reminds me of the story that Mike told at the cremation service two days ago. When clearing out Grisha's cupboard, they found each jacket had three pens and over half the jackets had been awarded the Order of Australia. Our next speaker is Phillip Law, Antarctic scientist, educationist and another one who shared a friendship with Grisha for more than 30 years.

PHILLIP LAW Thank you Bill. Ladies and Gentlemen, it's quite obvious what a remarkable person Grisha was. He combined high intelligence with dynamic mental energy and a penchant for getting things done. With his creative mind he was always looking for new things to do or for ways of improving old things, but above all he had a passion for friendship. He worked at maintaining friendships, something most of us are either too lazy or too careless to do. He knew more people than anyone I have ever met. Some 30-odd years ago Grisha organised a luncheon group, comprising professional associates from ICI and from outside the company. It met once a month. The club exists today as vigorous and lively as ever. Most such groups last a few years and then fade out, but Grisha held this group together with his enthusiasm and his organising skills. It constitutes a forum for intellectual discussion and camaraderie that is unique. It is up to us surviving members to ensure that, as a memorial to him, the Sklovsky lunches will continue on into the distant future. Grisha's concept of the high responsibilities that friendship entails led him to go out of his way to help people in a variety of situations. To a busy man, and Grisha was an exceptionally busy one, the most valuable commodity is time. Grisha was unsparingly generous in devoting time to anything that concerned his friends. He thought of ways of assisting them and their projects, their concerns, their welfare, whether or not they actually called for assistance. In a broader sense this attribute led to his deep sense of responsibility of service to the community. His Curriculum Vitae lists a multitude of institutions to which he contributed time and effort, but I wish to comment upon one in particular—the Royal Society of Victoria—for which he had a deep attachment.

But first I must mention his long and important successful political campaign to block off a highly undesirable development plan for Camberwell Junction. It is appropriate that we are meeting today in this venue. He became a

member of the Royal Society in 1963 and was elected to its Council in 1967. A new position of Development Manager was created and Grisha undertook the honorary duties of this position with zeal — working to build up membership and to devise ways of promoting the Society. In particular he worked to rejuvenate it, broadening the scope of its monthly lectures to appeal to members. In 1983 he became Vice-President and then was elected President, serving from 1985 to 1987. All in all he helped transform the Society from what was a rather stodgy, sluggish body into a vigorous and lively organisation.

I personally owe Grisha a debt of gratitude for having conceived the idea of holding a Society Symposium to celebrate my 80th birthday and for having carried it through successfully, complete with a published report of the proceedings. Grisha had a keen interest in Antarctic affairs, partly due to the fact that his brother-in-law, Jean, was the administrative officer of Expeditions Polaires Francaises, a French Polar organisation led by Paul-Emile Victor. Grisha visited the station 'Dumont d'Urville' in Antarctica on two summer relief voyages of the French expeditions. He acted as liaison officer in Australia for the years when these expeditions used to leave from Melbourne. And when an Antarctic Treaty consultative meeting was later held in Canberra, Grisha took on the job of English/French interpreter at the Treaty. My friendship with Grisha goes back well over 30 years. I and his numerous friends mourn his passing deeply but remember with affection his warm, generous, outgoing personality and his considerable contributions to the Melbourne society.

WILL DARVALL   Our next speaker is Liz Taylor — physician, scientist and family friend, who will speak on behalf of the Taylor family.

LIZ TAYLOR   Grisha Sklovsky was an educated man. He loved education, being educated, and educating. He never questioned if one should be educated and Celia explained that he loved an educated woman. When the Sklovsky family asked me to speak as a token educated woman my humility took a dive. I knew how many here would be educated and I felt quite flattered. Then swift and direct as Grisha could be, Michael Sklovsky quickly reminded us that Grisha loved a bimbo too. Stevie, Daniel, William and Daisy — Grisha and Celia's beloved grandchildren — I wonder if they remember again

that Grisha used to play with my children and that they loved it when Grisha would ask 'What colour is this?' 'Red' the children would call it. 'No' Grisha would say, his eyes twinkling, his smile broadening, and the children laughing, Grisha would say 'It's green'. Why was this so amusing? One possible explanation was that it was so incongruous that Grisha, so rock solid, so reliable, didn't know something as fundamental as his colours. Grisha was rock solid, reliable, almost infallible, in his relationships with his family and friends particularly. Consider a phone call when Grisha answered 'Sklovsky'. 'Oh dear' you thought, 'I've interrupted in the middle of something important'. 'Hello Grisha this is Liz.' 'Hello Liz.' It sounded like he had been waiting for you to call all day. Then he would give you a piece of information, a story, remind you of a relevant piece of music or TV programme, or share a family incident, or something of his very precious Celia — something that he'd been saving just for you until the moment you called. Then you realise that that D flat 'Sklovsky' was because he had been waiting for you to call and he hadn't been able to share with you his particular gift earlier. He was there if you needed advice. Someone you could refer a particular problem to or who could help you with information that you required. Always waiting to help, to inform, or to educate. Rock solid and entirely reliable, his concern for us all was all encompassing. Equally his enthusiasm for his various works was all encompassing. He was always educated in the areas in which he was involved. He always seemed to know such a lot and he loved to know things. Celia told me a story last Sunday of an incident that occurred early in their relationship. Grisha had come to the house where she was staying and he and his friends sat down to discuss French literature and other things in French. Celia was feeling rather lost and left out. This was a long time ago. She went out to the kitchen and confided in her hostess that she felt uneducated and uneasy in this place of educated people and to her horror her hostess relayed this to Grisha, who'd appeared at the door with, quote, 'his funny round face and quaint clothes'. On hearing this Grisha started to laugh. 'That's wonderful' he said. 'We've been talking about these things for so long but we've never been able to impress anybody before.' How then could he not be here? Is this like the colour game, incongruous to our fundamental concept that Grisha is always there? I don't think so. Grisha has spent his life educating us

about his passions. He's laid a rock solid foundation for us. We can act as the bricks and the mortar, to build on that foundation and continue to build the edifices of his works. His most recent passion was the work of the Institute of Reproduction and Development at Monash. Again Grisha was able to see the extent and ingenuity of science being carried on in this Institute. He was becoming quite well educated in the variety of biosciences conducted there. His passion for the work of the scientists in the Institute can be built upon. It's most fitting that a research scholarship in the Institute of Reproduction and Development will be set up in Grisha's name to continue his tradition of educating. However, there will be continued and less tangible ways to build on Grisha's educational foundation. We will continue to be his all encompassing friends and he will continue to be our all encompassing friend and rock solid foundation.

WILL DARVALL Our next speaker is Zelman Cowan who, like everybody else, shared a warm friendship with Grisha for a long time.

ZELMAN COWAN Friends, at the beginning of each year a new wall chart is placed in my office and it marks appointments, speeches and commitments. As in earlier years, the chart for this year, 1995, has eleven red stickers bearing the words 'luncheon club'. The first date for this year is 7th February. I had anticipated that on that day Grisha would call for me at my office in Treasury Place. That we would drive to the Hotel in North Melbourne, talking all the way. That we would have an excellent lunch with talk ranging with the club members over many topics, whereafter Grisha, who managed the whole thing, would drive me back, both of us talking all the way, to Treasury Place. That, as I tell you, is scheduled for 7th February. No doubt that lunch will still take place on that day but there will be no Grisha. How things will develop no one of us yet knows. It's hard to see it without him, without the imprint of his style, his zest and his enthusiasm. Also a sign to an early date in this year is a visit to CSIRO, concerned incidentally with the information super highway, in company with Grisha. I suppose all we can say is that we work and plan on the assumption that life goes on forever. I don't recall where or when it was that I first met him. It was some time in my Melbourne days when I was at the University of Melbourne. That was between 1951 and 1966, so that there

is a wide margin for error, and in those years he was with ICI. It must have been at some time in this period that I joined the luncheon club. Then in 1966 we went away from Melbourne and I did not permanently return, we did not permanently return, until August 1990. In the years away I remained on the occasional list of the lunch club members and, typically, a list of dates came to me wherever I was each year. I came on occasions when dates coincided with time in Melbourne. Then, not long after our return to Melbourne in August 1990 to settle, we came to Grisha's 75th birthday celebration. It was an enormous and a lively party and I remember the long rhyming count, a count of Grisha's life and style, which was recited with great gusto amid roars of laughter and appreciation. That great party really gave me some picture of the range of Grisha's friendships, of his interests and of his activities. And it set the course for the shared years of life that we were to enjoy together. And it happens oddly, but perhaps aptly, that we last met and talked on my 75th birthday party late last year. We had shared interests in the Institute for International Affairs, though in later years he spoke to me of his concerns about it and, after a very busy and long involvement in its management and administration in Melbourne, he was talking about some reduction of his activities in it. His long enduring interest in the Institute was a reflection of his lively concern with international affairs and relations. He was born into pre-revolutionary Russia and he lived to see the Soviet Union disappear. In its wake there are many things occurring in various parts of the world which he and I, from a generally shared perspective, did not much like. The disappearance of the Soviet Union certainly has not heralded a glad confident warming.

Those of us who have known him, the many, many of them, are all aware of his extraordinary network of friendships and that's been remarked again and again today. He worked at those friendships and acted upon the admonition of Dr Samuel Johnston, that friendship should be worked at, should be kept in constant repair. Sometimes I have to say at least once 'I resisted'. I remember how, not long after my return to Melbourne, he sought to recruit me to his tennis group. For some reason I resisted and procrastinated. He must have come at it a dozen or twenty times. I'm not sure why I didn't obey. Not having played for some years it may be that I was feeble

enough not to want to take up the challenge and the test of starting again. And then, as has been said, in recent years he became involved as chairman of the management advisory board of the Institute of Reproduction and Development of Monash. He drew me in as a patron of the Institute. As a lawyer I've had a long concern with a number of the matters which concern it. One of the last things we talked about was support for the Institute. He was enthusiastic about its work and its purposes and proud of his association with it. I suppose the point comes back very clearly, he was a great enthusiast and this masked the fact that he was after all nearly 80 years old. It is good that our memories of him are of a man at the top of his formidable form. When I spoke to Celia on hearing of his death I said that I felt bad. She queried the words and perhaps I expressed myself in an unsatisfactory way. What I meant was that I was deeply saddened, disturbed by this sudden loss of a friendship which gave me and those who shared it great comfort, that his death has left a void which will not easily be filled. Like many who are here today I am grateful that our lives touched as they did. He had, as I say again, a genius for friendship as many of us know and I am very glad to have been a beneficiary.

WILL DARVALL   Our second last speaker is David Dekretser, Director of the Institute of Reproduction and Development at Monash.

DAVID DEKRETSER   Thank you Celia and family for giving me the honour to participate in this ceremony. I've only come to know Grisha over his latter years, really since 1992, when I first met him in his role on the advisory board of the Centre for Early Human Development, something that, through the friendship of Michael and Alan Trounson, Grisha was recruited to. And when I first met him I wondered who was this unusual man and the more I learnt it was borne out, he was a truly unusual man. And as I got to know him more and more it became evident that he was in fact the person to be the inaugural chairman of the Institute's advisory board which was set up in 1993. This was a very important role, as we pulled together several successful but independent research groups to form an Institute, as we sought to develop its structure, its public image and to establish its niche in a very competitive research arena in Melbourne. Grisha loved the challenge. It was very obvious as the time went by that we had

made a wise choice. He was the most enthusiastic supporter of the Institute. He was inquisitive, always seeking information. Seeking to understand the complex relationships between the Institute, the Faculty, the University and the hospital—quite a lot to get together. And he provided us with very wise counsel in developing the structures in the formative phases of the Institute. And he had a great sense of humour as everybody has mentioned. A quip or a comment was just absolutely right. And on one occasion, when we'd finalised this giant structure of relationships between the board and the University, a cartoon arrived on my desk from Grisha depicting a pyramidal structure of individuals with the caption 'So now we're organised, what do we do?' And on another occasion after some very, very frustrating delays with the bureaucracy within the University which was causing us quite a lot of despair, another cartoon arrived. This time it was a picture of a heron, and you may well have seen this, with the head of a frog in the mouth of the heron, with the arms of the frog grasping at the throat of the heron, with the title 'Never give up'. A comment really which personified his approach to many things. He continually joined in the activities of the Institute. He was keen, as Liz has indicated, to understand the scientific work and he came to know many of us very well, members of the staff and the advisory board. And he sought every opportunity to promote the Institute to you, his very wide circle of friends. He created opportunities for our scientific staff to talk at public meetings and in fact he had planned a meeting, which I hope will go ahead, with the Royal Society of Victoria later this year in March, to enable us to talk about the issues of reproductive medicine which impinge on our society. He introduced us to many influential friends. He was to us the information super highway, from that point of view, as he sought funds for the Institute. And I hope you will forgive him for what he has done to you in pestering you about the Institute in the hope of involving you in its future development. The Institute really has been very fortunate to have such a man as its inaugural advisory board chairman and his influence will be greatly missed. To recognise his contributions to the Institute, as Liz has indicated, we hope to provide a post-graduate scholarship called the 'Grisha Sklovsky Scholarship'. I think such an award would embody Grisha's interest in young people and the provision of funds to enable post-graduate

students to continue their intellectual development would certainly be in keeping with his philosophy. On a personal note, it has been fortunate to get to know him well in many delightful discussions that we had, often on the weekend, often over a glass of whisky, often after a game of tennis, and as I learnt more and more about him it's been wonderful to piece it all together today. I learnt how he dealt with the adversity of his visual problems and his hips. And he was eternally grateful to the medical developments which permitted him to enjoy his weekly tennis forays, they were indeed a highlight. And he continued his interest in the Institute really right up to his death because on the Monday we were to meet for lunch with Sam Lipsky and I'm sure that Sam knows it would've been a lobbying session with regard to the Institute. Both he and Celia were welcoming hosts and it was interesting, when I first met Celia, I thought 'I know her from somewhere'. Yet I hadn't met her. Then it came together because, of course, Celia is Barbara's sister and Barbara I had known in younger days 'cause Bill and I shared our time together in doing medicine and many other fond memories. It was very obvious that his family was important to him. He was unashamedly proud of the achievements of his children and his wider family and in this   sense we at the Institute felt some of his pride in our achievements. It was indeed an honour and a pleasure to have known the scholar and gentleman.

WILL DARVALL   Our final speaker is my brother Peter Darvall, nephew, protege and Claytons poet.

PETER DARVALL   In 1938 a charming young Australian woman was in Europe and she went to the Cinema in Lyon. At interval she decided she needed a cigarette and required a light. An alert young man with thick greasy hair, a loud suit and thick spectacles was alert to her needs. Last week, in 1995, a delightful and exotic old gentleman wearing handsome blue pyjamas and carrying a bag of salami and smelly cheeses and, most of all, telling jokes, appeared at a place which they tell us has Pearly Gates. In 57 years, in those 57 years, he enriched and added value to all of our lives. In the first 10 of those only Celia was the occasional beneficiary but, in the remaining 47, we have all been privileged. He was, as you have learned and as you know very well, both interesting and interested, delightful, and most of all took delight in everything and delight, I think, is the word that most sums Grisha up. One thing we've all learnt from him is to take enormous pleasure in little things. We can all remember the way he would shake with mirth at a quip and how he would laugh uproariously at his own jokes. The delight in waiting for Grisha's first joke at a Christmas party. The delight he took in all little children. The delight that most recently he experienced at Musica Viva when at interval he went up to his old friends and, quivering with excitement, almost bouncing, said 'Don't you notice anything different about me?' He couldn't wait to tell them that for the first time in his whole life he was not wearing glasses. If life is a party then Grisha was the life of that party and I am the nefarious poet referred to earlier by Sir Zelman. I won't burden you with the whole of it but I'd like to read some bits of it because it is about the party theme, it's entitled 'The Party Boy'. Copies of this poem will be available at Celia's later. In that poem I listed the Culture Party, the Party Lunch, the Camping Party, the Christmas Party, the Party Politic—and you know how much enjoyment he took out of even those politicians that were entirely opposed to his own views—The Prospect Hill Party, the SBS Party, the ICI Party, the Tennis Party, in short 'Life's a Party'. There are a couple of allusions in this poem, the Ron that is referred to is Ron Taft, the Pip that is referred to is my eldest son, and the gardening that is referred to is something that Grisha tried once and decided that he didn't like. Extracts from a poem entitled 'The Party Boy'.

Our Grisha is gregarious enjoying parties various
I'd like to take a little time recalling some in halting rhyme
I know that you'll admit that we have all had jolly times with G
I'll make a low key gentle start and mention first the culture part
Or party should I rightly say since Grisha knows no other way
Yes everywhere that Grisha goes it seems that everyone he knows
'Good God there's X' he'll likely say at interval of some new play
'We shared a lunch in '43 I'm sure that he'll remember me'
And that he does who could forget none of us has ever yet found someone that he hasn't met

Often he's been known to snore at concerts
in preparation for the hectic round all
through the break when he must be most
wide awake

To swap some jokes and see his mates and
check on all his luncheon dates

The party lunch I must report the endless
quest for a better sort

Grisha bent on discovery of new locations
culinary

When Grisha's cronies all arrive a struggling
bistro comes alive

Or hotels off the beaten track with Osso
Bucco out the back

I must record a special trip when Grisha
with his first new hip

Leapt out of bed to lunch with Ron and
promptly slipped and fell upon the mossy
step and with a crunch invented thus the
one hip lunch

On summer and the seaside camp, Grisha
put the party stamp

If you want to laugh then you should seek
my Uncle G at the Wild Dog Creek

There's many who could truly tell camp
vinex yes I knew it well

Black plastic tied with bits of string vinex
for most everything

Mats and covers, flaps and sheets, table-
cloths and flimsy seats

Tattered canvas and other such given a
cultured modern touch

Though some would view him with a smile,
his plastic sandals set the style

Bronzed surfie G on his rubber mat or by
the pools in his goggles sat

Checking out the latest news and sharing
wide his well formed views

Things were not as they might seem that
so-called camping had a theme

If to dull life some style you bring anyone
can be a king

Smelly cheese was Grisha's way to keep the
blowies well at bay

The mozzies despite their fierce attack
couldn't pierce his hairy back

With fish and chips some crayfish cook
improve the beach with the best new
book

Raining the vinex will keep us fine with
salami, tongue and good red wine

By Wild Dog Farm a bumpy court, a tennis
of a different sort

Cheating, tricks and sleights of hand,
cackling from his merry band

Once little Pip was quite amazed when

from the creek his line was raised

On which he'd caught a big red carp those
in the plot or who were sharp knew that
the creek was far too small to have this
ocean fish at all

Under the bank that noise was G shaking
with his usual glee

We recognised the fish all right, he'd
bought it in the town last night

The parties at old Prospect Hill have
famous been and famous still

The garden flowering with his art Celia
plays a minor part

Green fingers G just simply loves to slip
into his gardening gloves and spend a
day with birds and bees, 'Hello flowers
and hello trees' but best he likes the
lunching bit, so for an hour or four he'll
sit to shameless chat and laugh and shirk
while Celia does the heavy work

As handyman and builder too Grisha's
skills are known to you

He often will philosophise it takes brains
to organise adding then with awful smirk
any bloody fool can work

Grisha has a concept neat everything
should be a treat

Life's a party, he hates to miss the news in
full pursuit of this he listens to all times
of day, here or there or on the way

At dawn he nearly jumps for joy at the
rustling sound of the paper boy

The sayings of old chairman G often seem
astute to me

He has been wrong I will admit but we
would never dwell on it

I'd better stop this complex tale to tell it
all I'm sure to fail

Anyhow you get the gist many party types
I've missed

Suffice to say from you and me we'll miss
the party loving G.

I want to hark back to that delight. Of course
we're sad that he has gone and we will miss
sharing that delight with him, but that delight
has been promulgated, I know, in my own life
and I know the lives of so many others. We've
been very lucky and, Celia, thank you for being
so absolutely brilliant in 1938.

WILL DARVALL Celia and many others are
naturally thinking about the possibility of a
biography and any expressions of interest along
those lines please direct them towards Celia.
Wild horses and broken legs would not have

stopped Grisha attending this incredible celebration for he would have loved the recognition. But the family and I know that there's one thing that would've gladdened his heart right now. Let's have three cheers for Grisha. That is the end of our proceedings.

LINEAR DUNES AT WILSONS PROMONTORY AND SOUTH-EAST GIPPSLAND, VICTORIA: RELICT LANDFORMS FROM PERIODS OF PAST ARIDITY

S. M. HILL* & J. M. BOWLER

The University of Melbourne, School of Earth Sciences, Parkville, Victoria 3052
*Present address: The Centre for Australian Regolith Studies, The Australian National University, Canberra, ACT 0200

HILL, S. M. & BOWLER, J. M., 1995:12:31. Linear dunes at Wilsons Promontory and south-east Gippsland, Victoria: relict landforms from periods of past aridity. *Proceedings of the Royal Society of Victoria* 107 (2): 73–81. ISSN 0035-9211.

Within the low-lying areas of northern Wilsons Promontory and south-east Gippsland extensive areas of linear dunes are preserved in the modern landscape. The dunes are morphologically similar to the linear dunes that have been described from arid and semi-arid regions of Australia. The trends of the dune crests reflect a predominance of west to north-westerly winds during their time of formation, which is in contrast to the prevalence of south-westerly onshore winds experienced today. These dunes are relict features that developed during the more arid, continental conditions associated with glacial periods. This evidence supports interpretations involving a substantial southerly expansion of the inland dune systems during periods of past aridity.

THIS paper describes the linear dunes and some of the associated landscape features in the northern part of Wilsons Promontory as well as similar dunes from elsewhere in south-east Gippsland, Victoria.

Extensive areas of linear dunes are a major feature of arid and semi-arid areas of Australia (Wasson 1986; Bowler & Magee 1978). These dunes are essentially relict features and were active in arid and semi-arid climatic conditions during glacial periods, such as between 25 000 and 16 000 B.P. when linear dunes were last active (Bowler 1976; Gardner et al. 1987). Some dunes are still active in highly arid areas such as the Simpson Desert (Wasson 1983), and where stabilising vegetation has been cleared (Bowler & Magee 1978). The orientations of Australian continental dunes broadly conforms to a continental scale anti-clockwise whorl (Jennings 1968; Wasson et al. 1988). Sand transport has been towards the east in the southern areas, as in the Mallee, towards the north in the eastern part, as in the Simpson Desert and towards the west in the northern part of the whorl, as in the Great Sandy Desert (Fig. 1).

Restricted areas of similar dunes also occur in temperate regions of Australia that no longer experience an arid climate. Examples include: the 'relict terrestrial dunes' from north-eastern Tasmania (Bowden 1983), the 'old dunes' on King Island (Jennings 1959), the 'extensive areas of linear dunes' on Flinders Island (Sutherland & Kershaw 1971; Kershaw & Sutherland 1972) and the dunes at Cranbourne in Victoria (Bowler 1990). These features are relict forms reflecting the extension of arid conditions into these areas, during glacial periods (Bowden 1983; Bowler & Wasson 1983). The location of south-east Gippsland, on the periphery of the Australian continental region is in a location likely to have been greatly affected by climatic oscillations during the Quaternary.

We will first describe the dunes from the Wilsons Promontory area, followed by an extension of these features further north in south-east Gippsland. We will conclude with a discussion of the palaeo-environmental implications for this region. Fig. 2 shows a regional map of the area considered in this paper.
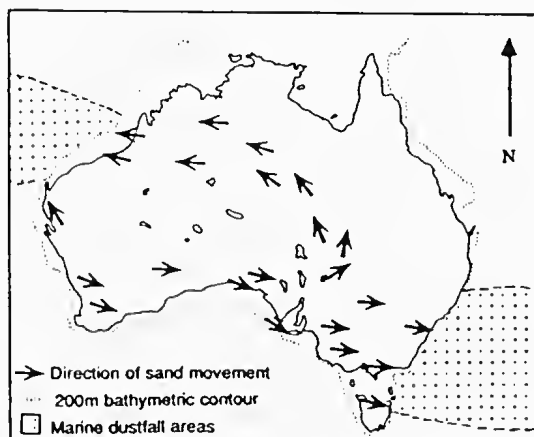
Fig. 1. Australian Pleistocene dune map, showing the areas of terrestrial dune activity and the continent scale anticlockwise 'whorl' pattern of dune trends. (Modified after Bowler 1976; Wasson 1988.)
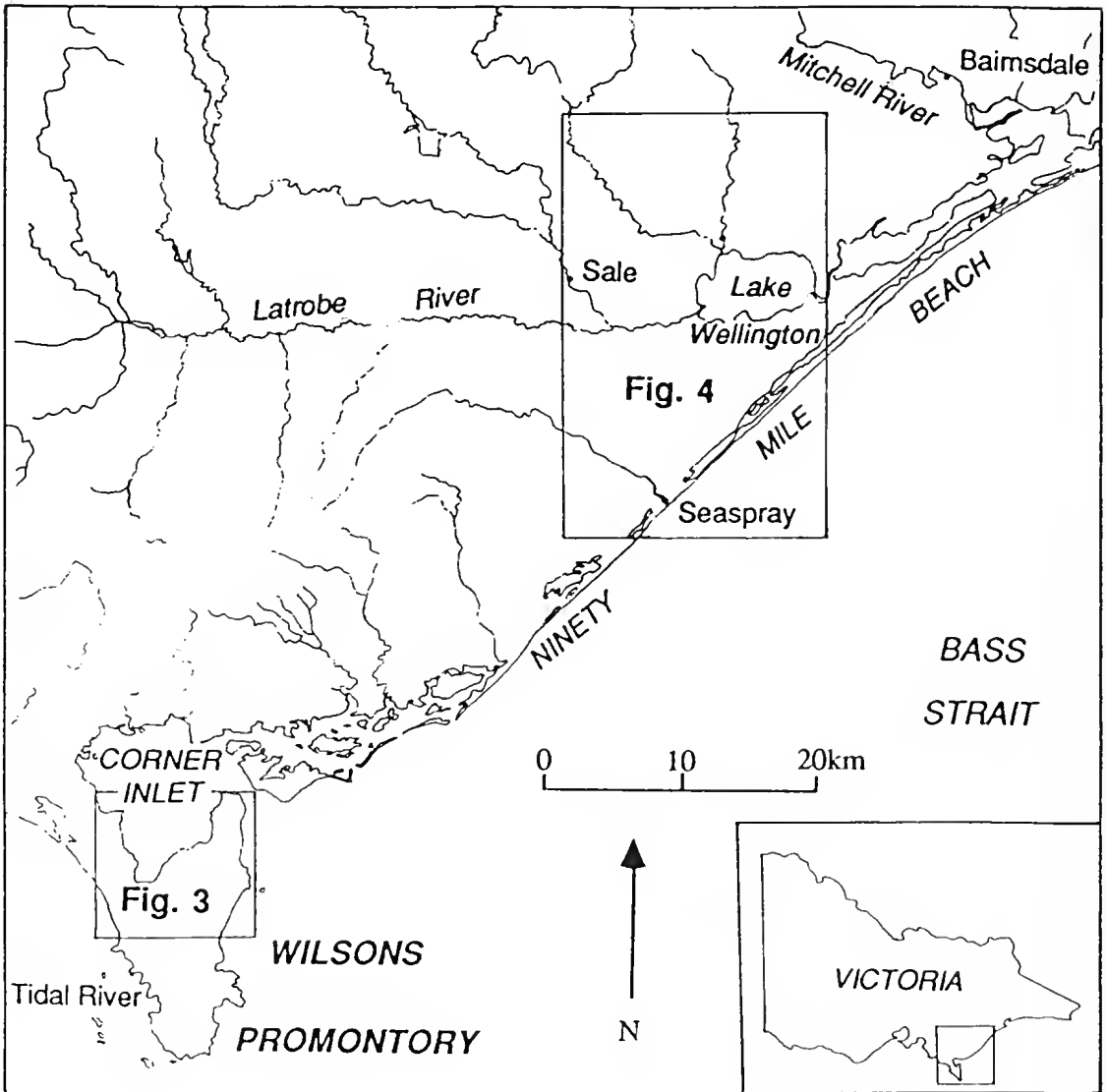
Fig. 2. Regional map of south-east Gippsland showing the areas considered in this paper.

LINEAR DUNES OF
NORTHERN WILSONS PROMONTORY

Landscape setting

Wilsons Promontory, the most southerly point of the Australian mainland, lies approximately 230 km southeast of Melbourne. It presently experiences a temperate maritime climate. The annual temperature ranges from 0–38°C, with an average of 14°C in summer and 8°C in winter. Annual rainfall has a slight winter maximum and ranges from 100 cm on the west and south coast to at least 150 cm at higher altitudes. West-south-westerly on-shore winds presently prevail, with occasional strong winds from the east and southeast.

Wilsons Promontory consists of a series of granitic highland ridges with adjacent low-lying areas of Cenozoic sediments. The coastal lowlands mostly consist of swampy plains, such as along the southern margins of Corner Inlet and inland of Five Mile Beach, and of dune fields such as on the Yanakie Isthmus. Fig. 3 shows the main geomorphic units of northern Wilsons Promontory.

Weathering of the granites, since their emplacement in the Late Devonian, led to the development of deep weathering profiles by the Mesozoic. Since the mid-Cretaceous, stripping of the deeply weathered material has been greater than the continued weathering, resulting in the present geomorphic features of the granite areas (Hill 1992). The landscape features of the granite areas of Wilsons Promontory are featured in Hill (1992, 1994, in press), Hill & Joyce (1995) and Hill et al. (in press) and will not be discussed in detail here.

Low angle slopes of colluvium and alluvium extend from the granitic highlands onto the coastal lowlands. These mainly consist of materials such as quartz sand and kaolin-group clay minerals derived from the weathering of the granites in the highlands. Tuddenham (1970) considers the possibility that these deposits originated during slope instability associated with cold (periglacial?) conditions during glacial maxima. Whilst periglacial conditions may have extended to the higher peaks of the region during glacial periods, no conclusive evidence has been found to support this suggestion. Hill (1992) found evidence for several periods of slope instability up to the present time and concluded that the extensive development of these deposits is mainly due to a combination of factors: (i) the steep and dissected terrain; (ii) an abundance of weathered material with reduced bulk density and shear strength; (iii) a tendency for the area to experience periods of torrential rain; and (iv) the removal of the vegetation cover by forest fires.

Calcareous and siliceous sands

Calcareous and siliceous sands of marine and aeolian origins occur along most coastal margins of northern Wilsons Promontory. Beaches to the west, such as Waratah Bay, have modern deposition of calcareous sands derived from submarine ridges of calcareous sediment. Beaches on the east coast, such as within Corner Inlet, are characterised by siliceous sands transported from the east. Localised areas of siliceous sand along the west coast represent material deposited before the development of the Yanakie Isthmus, which became a barrier to the movement of further siliceous sands from the east. Aeolian and marine reworking of many of these siliceous sands, formed extensive flat-lying sand sheets, such as that west of the Vereker Ranges (Fig. 3).

Sequences of beach ridges on the east coast of Wilsons Promontory represent progradation of the coastline since the post-glacial marine transgression, 6500–4000 B.P. (Tuddenham 1970; Thom & Roy 1985). The most extensive development of beach ridges occurs in the Entrance Point area, where Tuddenham (1970) made a detailed study of the more than 80 ridges that have filled the original embayment. The granite bluff backing the ridges represents a coastline predating progradation.

The calcareous sands of the west coast of Wilsons Promontory form beaches and aeolian calcarenites. Calcareous dunes are parabolic, with dune axes trending to the west-south-west (Fig. 3). This trend conforms to the present west-south-westerly on-shore wind resultant. Recent movement of these sands has progressed westwards across the width of the southern part of Yanakie Isthmus and into Corner Inlet (Fig. 3).

Linear dunes

Narrow-crested, east-west trending linear dunes extend across much of the coastal lowlands of northern Wilsons Promontory. Early work in this area by Tuddenham (1970) and Wallis (1981, 1987) made brief reference to these dunes. Oyston (1988) recognised the significance of similar dunes in the northern Yanakie Isthmus. Hill (1992) later found these dunes to be much more extensive than was previously thought, with the recognition of similar features on the coastal lowlands adjacent to Corner Inlet and Three Mile Beach (Fig. 3). Dunes do not occur on the extensive coastal plain backing Five Mile Beach, probably due to its position on the leeward side of the Vereker Range.

The dunes are best recognised on aerial photographs. They appear as elongate rises, vegetated with a shrubby woodland surrounded by lower poorly drained swales characterised by a swampy heathland community. The dunes originate on the plains and extend up the lower slopes of adjacent granite hills, usually terminating below 20 m above present sea level. They consist of well-sorted and rounded, fine to medium grained quartzose sands. Dune crests are commonly less than 1 km long and spaced between 200 and 500 m apart. They are characterised by a well-developed sandy podzolic soil.
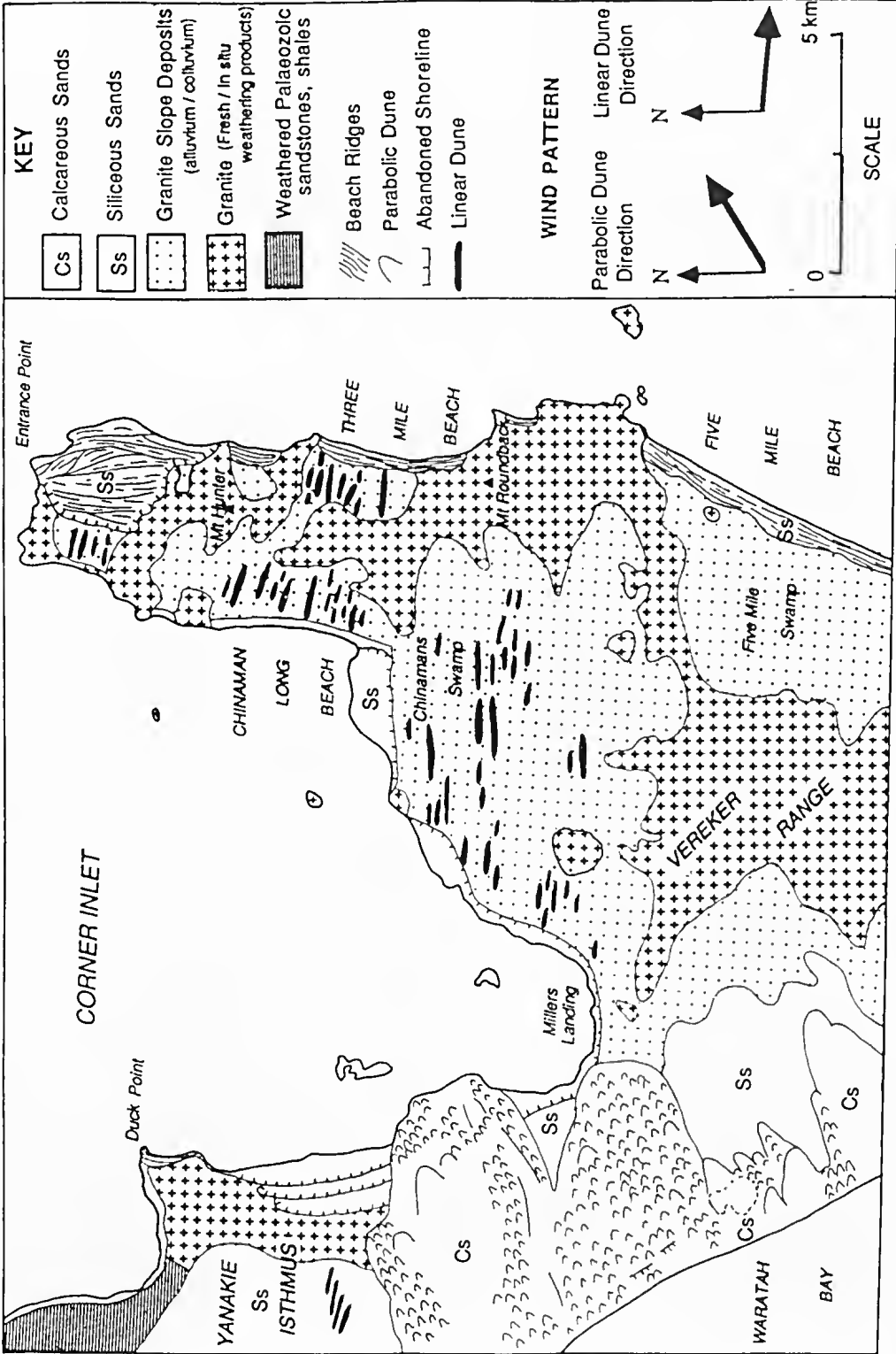
Fig. 3. Geomorphic map of northern Wilsons Promontory (after Hill 1992), showing the main landscape features and the resultant trends of the recent dunes in comparison to the linear dunes.

Oyston (1988) suggested that the source of the sands in the dunes was the marginal marine siliceous sands found to underlie the Yanakie Isthmus area. The ultimate source, however, would be the granites of the Wilsons Promontory batholith with possible contributions also from the weathered Palaeozoic sandstones intruded by the batholith. Small amounts of tourmaline, a common accessory mineral in the Wilsons Promontory granites (Wallis 1981, 1988), support the ultimate granitic source hypothesis. The marginal marine siliceous sand source suggested by Oyston (1988) would be the proximate source of sand derived from more recent erosion. The granite slope deposits would also contribute siliceous material that is then reworked. Aeolian and marginal marine reworking of the slope deposits have removed the clay fraction, leaving quartz sand to be moved across the surface of the coastal plains developing the linear forms.

The alignment of the linear dune trends is between east–west and northwest to southeast, reflecting a mean west-northwesterly wind resultant (Fig. 3). This is in contrast to the modern on-shore, west-southwesterly resultant that is reflected in the Recent calcareous parabolic dunes. The high degree of podzol soil development on the dunes, compared to the poor development of profiles on the Holocene calcareous dunes suggests that the linear dunes are pre-Holocene. Other features indicative of antiquity include: degraded rounded crests, well-developed vegetation communities, truncation by post-glacial shoreline features and their stratigraphic position underlying transgressive calcareous dunes in the northern Yanakie Isthmus area.

DUNES AND SAND SHEETS IN SOUTH-EAST GIPPSLAND

The environment represented by the Wilsons Promontory dunes finds additional expression in linear dunes further north near Seaspray in South Gippsland (Fig. 4). Here a series of west to east trending sand ridges occur between the uplands of the South Gippsland ranges and the coastal sand barriers. Previously interpreted as relict coastal features (Jenkins 1968), a significant percentage of the inland dunes are almost certainly of terrestrial origin.

High level sand ridges mapped by Jenkins (1968: plate 3) extend over a large area of South Gippsland. They occur from Monkey Creek in the south towards Longford in the north. North of Lake Wellington they extend from Perry Bridge

in the south to Lindenow South near the Mitchell River in the northeast.

The distribution of crestal ridge trends (Jenkins 1968: fig. 66) varies from an E–W direction in the north to WNW–ESE in the south. Near Seaspray, the dune trends intersect the present coastline at an angle of 55–60°. South of Lake Wellington, trends are mainly E–W remaining closely parallel to the shoreline. North of Lake Wellington, dunes on the eastern (downwind) side of the Perry River trend mainly between 70–80°.

Jenkins, sensing the possibility of a terrestrial origin, used several lines of argument to associate the dunes with a coastal marine rather than terrestrial origin. These arguments are summarised below.
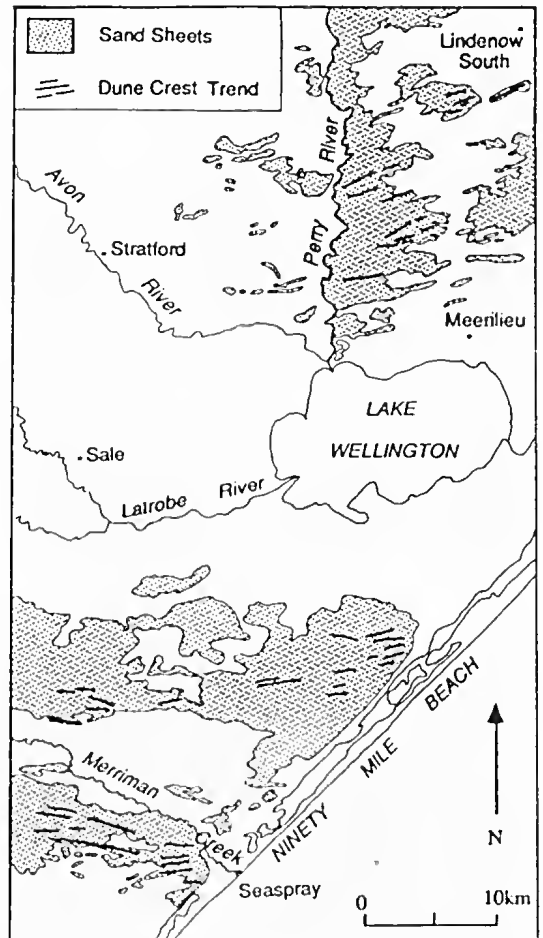
Fig. 4. Map of the Seaspray to Lindenow South area, showing dunes and sand sheets (after Jenkins 1968).

Marine hypothesis

1.   Different fields show somewhat different trends. Those south of Merriman Creek have a more southeasterly trend than those further north as along the Princes Highway between Stratford and Bairnsdale. This was taken by Jenkins to be consistent with *the direction and successive position of the former coastline.*

However, it is only in the north that dune trends parallel those of the shoreline where both trend approximately east–west. In the south, near Seaspray, dune and coastline trends differ by up to 60°. The argument based on parallel accordance does not hold.

2.   Structures in the lower parts of the ridges are horizontal or dipping at low angles more consistent with beach or beach ridge deposits. However, sub-horizontal, low angle conformable deposition is also characteristic of sand sheets and low sand ridges where avalanche bedding does not develop. The upper parts of the ridges and crestal trends are certainly wind controlled.

3.   Sediment in the lower sections is too coarse to be wind deposited with *areally extensive beds of fine gravel being common throughout* (Jenkins 1968: 82). This reference to an example described from Meerlieu lies closest to the undeniably marine features of the Lake Wellington-Victoria complex.

While this example is almost certainly representative of marine origin in this area, our discussion concerns the extensive dune and sand sheet features that extend for some 30 km north of Meerlieu. Within the area where dunes are found extensively on gravel deposits, basal horizons of gravel representing parent materials will be found in the core of ridges. A problem remains in differentiating between those ridges of genuine marine origins from those which bear no genetic relationship to shorelines.

Terrestrial hypothesis

1.   The dunes discussed here, with those defined from Wilsons Promontory, follow the same regional trends of glacial age dunes throughout southeastern Australia. Even the divergence in trends from slightly north of east in the Stratford-Bairnsdale area to south of east near Seaspray is precisely what might be expected from consideration of effects of local topography.

2.   The discordance between dune and coastal trends near Seaspray rules out a marine origin for the dunefield immediately south and north of Merriman Creek.

3.   The extensive sand sheets north of Lake Wellington are similar to others of known terrestrial origin. They are limited almost exclusively to the eastern or downwind side of the Perry River, suggesting an obvious sand source. This is precisely the relationship between stream and glacial age sandsheets known from other parts of southeastern Australia, as in the Shoalhaven River on the southern Tablelands at >700 m elevation where no relationship to Quaternary sea levels can be entertained.

DISCUSSION

Palaeo-environmental interpretation

The dominance of westerly to west-northwesterly winds during the formation of the linear dunes is similar to the wind patterns related to linear dune formation along the southern extent of the Australian continental dune field. The morphology of the dunes is also similar to the arid climate linear dunes, such as those of the Mallee region of northern Victoria (Bowler & Magee 1978). This suggests that Wilsons Promontory and south-east Gippsland once experienced a similar arid continental climate. Such conditions would have affected this area during glacial periods, such as the Last Glacial Maximum approximately 20 000 years B.P.

During the glacial periods with oceanic water locked in expanded polar ice caps, sea levels were considerably lower. The last glacial period resulted in sea levels to 150m lower than present (Jennings 1971; Chappell & Shackleton 1986). Most of the continental shelf was exposed: an extensive continental plain separated the Australian mainland and Tasmania (Orchiston 1979, 1984). Wilsons Promontory and south-east Gippsland would have then been over one hundred kilometers inland (Fig. 5). The region would have experienced a westerly continental wind in contrast to the southwesterly, on shore winds of today. At this stage the climate was also drier and winds were stronger (Bowler 1976; Bowler & Wasson 1983). The Bassian continental plain removed the moisture source for winds that now derive moisture from the waters of Bass Strait. Cooler sea surface temperatures during the glacial periods would also lower oceanic evaporation further reducing the moisture content of the winds. Such conditions, associated with colder winters, would lead to a significant reduction in the vegetation cover, enhancing deflation of the siliceous sands. Similar dunes almost certainly extended over the areas now submerged by the post-glacial marine transgression.

(a)

(b)

(c)
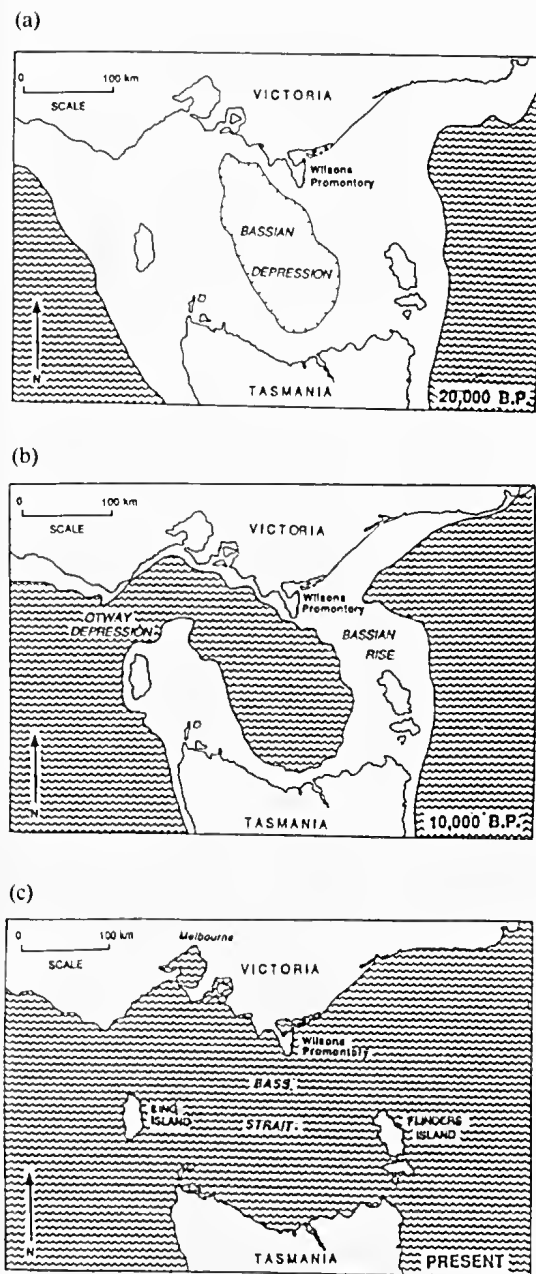
Fig. 5. Palaeogeographic reconstructions of the Wilsons Promontory region at 20 000 years B.P. (a), 10 000 years B.P. (b), and present day (c).

Although strong presumptive evidence exists for reactivation of dunes and sand sheets during the last glacial maximum (Bowden 1983; Sprigg 1979; Wasson 1986), the formation of the systems

described here may well predate that interval. The presence of strongly developed podzolic soils, such as on the dunes near Merriman Creek and at northern Wilsons Promontory, provides evidence of antiquity since dune stabilization. However, lack of data on actual rates of pedogenic development in this region prevents any accurate age definition. While remobilization during the last glacial maximum is to be expected, the history of these features almost certainly involves a much longer period.

A palaeo-geographical reconstruction of events since the last glacial maximum, approximately 20 000 years B.P., demonstrates successive changes in post-glacial shorelines (Fig. 5). This sea-level rise set the scene for modern coastal wind regimes and the present phase of calcareous sedimentation west of Wilsons Promontory. The associated increase in rainfall, decrease in the frequency of strong winds and an increase in vegetation cover, all assisted stabilisation of the linear dunes and subsequent podzolic soil development.

CONCLUSION

The evidence advanced here re-inforces previous interpretations involving a substantial southerly expansion of the inland dune systems during periods of past aridity. Seen at the continental scale, the location and orientation of the Gippsland and Wilsons Promontory dunes represent a substantial southeasterly extension of the inland systems.

A combination of increased aridity, lower temperatures, and increased windiness, greatly reduced the vegetation cover compared with that of today's and favoured greater aeolian activity in south-east Gippsland. These conditions permitted substantial modification of the landscape, including formation of linear dunes trending parallel to the predominantly west to west-northwesterly continental wind regime.

Since this time the sea has transgressed to its present position. There has been a decrease in windiness and an increase in rainfall and vegetation cover. Carbonate sedimentation replaced siliceous sedimentation along the west coast of Wilsons Promontory. Onshore south-westerly winds have since been responsible for aeolian reworking.

The evidence of continental aridity provided by these features has profound significance for understanding environmental evolution throughout southeastern Australia. The relatively high rainfall conditions that characterise these areas today appear to be quite unrepresentative of conditions that prevailed within the geologically recent past.

ACKNOWLEDGEMENTS

REFERENCES

BOWDEN, A. R., 1983. Relict terrestrial dunes: legacies of a former climate in coastal northeastern Tasmania. *Zeitschrift fur Geomorphologic, N.F., Suppl. Bd.* 4: 7–25.

BOWLER, J. M., 1976. Aridity in Australia: age, origins and expressions in aeolian landforms and sediments. *Earth-Science Reviews* 12: 279–310.

BOWLER, J. M., 1990. *From Sand Dunes to Tall Timber: Environmental Change and Human Impact in South Gippsland*. The South Gippsland Conservation Society Inc., 20 pp.

BOWLER, J. M. & MAGEE, J. W., 1978. Geomorphology of the Mallee region in semi-arid northern Victoria and western New South Wales. *Proceedings of the Royal Society of Victoria* 90: 5–26.

BOWLER, J. M. & WASSON, R. J., 1983. Glacial age environments of inland Australia, *SASQUA International Symposium*, 183–208.

CHAPPELL, J. & SHACKLETON, N. J., 1986. Oxygen isotopes and sealevel. *Nature* 324: 137–140.

GARDNER, G. J., MORTLOCK, A. J., PRICE, D. M., READHEAD, M. L. & WASSON, R. J., 1987. Thermoluminescence and radiocarbon dating of Australian desert dunes. *Australian Journal of Earth Sciences* 34: 343–357.

HILL, S. M., 1992. *The granitic regolith and associated geomorphology of Wilsons Promontory, Victoria*. Unpublished, BSc.(Hons) Research Report, The University of Melbourne, School of Earth Sciences, 66 pp.

HILL, S. M., 1994. Some granite landforms of Wilsons Promontory, southern Victoria. *The Victorian Naturalist* 111: 184–190.

HILL, S. M., in press. The differential weathering of granitic rocks in Victoria. *Australian Geological Survey Organisation Journal of Geology and Geophysics*.

HILL, S. M. & JOYCE, E. B., 1995. The landscape evolution and Granitic Regolith of Wilsons Promontory, Victoria. *Proceedings of the Royal Society of Victoria* 107: 1–10.

HILL, S. M., JOYCE, E. B. & OLLIER, C. D., in press.

Mesozoic deep weathering and erosion: An example from Wilsons Promontroy, Australia. *Zeitschrift fur Geomorphologie*.

JENKINS, J. J., 1968. The geomorphology and Upper Cainozoic geology of south-east Gippsland, Victoria. *Geological Survey of Victoria*, Memoir 27, 147 pp.

JENNINGS, J. N., 1959. The coastal geomorphology of King Island, Bass Strait, in relation to changes in the relative level of land and sea. *Records of the Queen Victoria Museum, Launceston*, 11, 37 pp.

JENNINGS, J. N., 1968. A revised map of the desert dunes of Australia, *Australian Geographer* 10: 408–409.

JENNINGS, J. N., 1971. Sea level changes and land links. In *Aboriginal Man and Environment in Australia*, Mulvaney, D. J. & Golson, J., eds., Australian National University Press, Canberra, pp. 1–13.

KERSHAW, R. C. & SUTHERLAND, F. L., 1972. Quaternary geology of Flinders Island. *Records of the Queen Victoria Museum, Launceston*, 43: 28 pp.

OYSTON, B., 1988. *The geology and Cainozoic evolution of the Yanakic Isthmus, Victoria*. Unpublished, BSc.(Hons) Thesis, Department of Geology, The University of Melbourne, 65 pp.

ORCHISTON, D. W., 1979. Pleistocene sea level changes and the initial Aboriginal occupation of the Tasmanian. *Modern Quaternary Research in Southeast Asia* 5: 91–103.

ORCHISTON, D. W., 1984. Quaternary environmental changes and Aboriginal man in Bass Strait, Australia. *Man and Environment* 8: 127–141.

SUTHERLAND, F. L. & KERSHAW, R. C., 1971. The Cainozoic geology of Flinders Island, Bass Strait. *Proceedings of the Royal Society of Tasmania* 105: 151–175.

THOM, B. G. & ROY, P. S., 1985. Relative sea-levels and coastal sedimentation in south-east Australia in the Holocene. *Journal of Sedimentary Petrology* 55(2): 257–264.

TUDDENHAM, W. G., 1970. *The coastal geomorphology of Wilsons Promontory Victoria: Implications concerning Quaternary sedimentation around the shores of Bass Strait*. Unpublished MSc. Thesis, Department of Geography, Sydney University.

WALLIS, G. L., 1981. *The Geology of the Wilsons Promontory Batholith, Victoria: a study of the composition, emplacement and structure of an S-type granitoid*. Unpublished, MSc. Thesis, Monash University, Department of Geology.

WALLIS, G. L., 1987. *Wilsons Promontory National Park Map and Walking Guide*. Gingko Publications, Melbourne.

WALLIS, G. L., 1988. Wilsons Promontory. In *The Victorian Geology Excursion Guide*, Clark, I. & Cook, B., eds., Australian Academy of Science, pp. 353–372.

WASSON, R. J., 1983. The Cainozoic history of the Strzelecki and Simpson Dunefields (Australia), and the history of the desert dunes. *Zeitschrift fur Geomorphologic Supplementband* 45: 85–115.

WASSON, R. J., 1986. Geomorphology and Quaternary history of the Australian continental dunefields. *Geographical Review of Japan* 59 (Ser. B): 55–67.

WASSON, R. J., FITCHETT, K., MACKEY, B. & HYDE, R., 1988. Large-scale patterns of dune type, spaeing and orientation in the Australian continental dunefield. *Australian Geographer* 19(1): 89–104.

SOME ASPECTS OF THE BIOLOGY AND BEHAVIOUR OF
PARALUCIA PYRODISCUS LUCIDA CROSBY (LEPIDOPTERA LYCAENIDAE)
AT ELTHAM, VICTORIA

IAN D. ENDERSBY

56 Looker Road, Montmorency, Victoria 3094

Field observations of the Eltham Copper butterfly demonstrate that anecdotal history has a basis in the biology of the species. Its preference for small food plants results from a strategy to optimise nocturnal travel distance consistent with providing sufficient biomass to complete development. Cases of overgrazing may cause larvae to cease feeding until regrowth occurs, thus delaying pupation and producing a bimodal adult emergence. The northwesterly aspect of the colonies is a consequence of the basking habit of the adult males and the vertical spiral flights are territorial encounters. Further study is required to elucidate the tripartite ecology of butterfly-food plant-attendant ant, to establish oviposition cues and the relationship between the ant breeding colony and its satellites where butterfly larvae are tended. The contributing factors to the low vagility of the species are yet to be determined but they possibly include patch dynamics of a restricted ecosystem and the as yet unknown mechanism for mate recognition. Colony management practices must recognise that delayed pupation due to overgrazing by some individuals means that there is no period when food-plants can be guaranteed to hold no life stages of this species.

PRIOR to a public campaign to preserve some areas of its remaining habitat at Eltham, little information had been published about the Eltham Copper butterfly, a subspecies of the Dull Copper *Paralucia pyrodiscus* (Rosenstock).

In his description of the subspecies, Crosby (1951) noted that the larvae fed on *Bursaria spinosa* (Pittosporaceae) with almost always a few small ants in attendance. At Eltham the adults emerged early in December and were most abundant about Christmas time with only occasional specimens remaining by early February. Common and Waterhouse (1972) identified the ant which attends the nominate species as *Notoncus* sp., recorded that the larvae feed at night, and noted that the life history and feeding habits of the subspecies are similar to those of typical *pyrodiscus*.

Appended to a deputation to the Minister for Conservation, Forests and Lands seeking preservation of the butterfly's Eltham habitat was a review of current knowledge (Crosby et al. 1987) which included:

the larvae have a distinct preference for plants of small stature, up to 0.5 m height;
it is possible that the subspecies is bivoltine;
adults are generally active on sunny days during late morning and early afternoon;
the habitat of all known Eltham populations is box–stringybark open forest on dry northwest aspects.

New (1987) commented that the larvae largely feed on plants which are stunted and apparently unhealthy.

A small, breeding colony had been known to the author for over ten years at a site in the West Riding of the Shire of Eltham, Victoria. In December each year adults were seen flying but few specific observations were recorded. Because of these regular sightings it was not realised that the species was considered to be endangered until that was reported in the local press (Calafuri 1987). Detailed observations of larvae and adults were then made between 28 March 1987 and 25 March 1988 and they provide the basis for this report.

STUDY AREA AND METHODS

The Eltham Copper Butterfly Draft Management Plan (Vaughan 1987) listed all known sites in a confidential supplementary appendix so as not to reveal their locations to unscrupulous collectors. Site E is the one where this study was done. It covers an area of 25 × 10 m and supports a fairly natural remnant of the local association of Long-leaf Box (*Eucalyptus goniocalyx*), Yellow Box (*E. melliodora*) and the introduced Cootamundra Wattle (*Acacia baileyana*), with an understorey of Sweet Bursaria (*Bursaria spinosa* var. *spinosa*), Gold-dust Wattle (*A. acinacea*), Drooping Cas-

sinia (*Cassinia arcuata*) and Small-leaf Clematis (*Clematis microphylla*).

Because of the reported endangered status of the species no specimens were collected or handled; no search for pupae or investigation of the ant nests was made; no translocation of larvae or marking of adults was attempted, even though these actions would have yielded additional valuable data. Only visual observations, times and air temperatures were recorded. Larvae were observed by torchlight but, as this often caused the larvae and their attendant ants to retreat, only a few bushes were sampled each evening to cause minimal disruption to feeding patterns.

Specimens of the ant were forwarded to the National Museum of Victoria and identified as *Notoncus enormis* (K. Walker, pers. comm.).

OBSERVATIONS

Larvae

Twenty-nine bushes, ranging in size from 340 mm to 2000 mm were host to larvae. Table 1 shows the height of each plant and the maximum number of larvae seen on it during the period. Those entries marked with an asterisk designate bushes where larvae were seen to be present but not counted; they have been attributed with only one larva so the total of 84 is probably an underestimate of the colony size.

During the period 28 March 1987 to 17 January 1988, 331 observations of larvae were made, and on 411 occasions no larvae were seen. Larval absence was due to inclement weather, complete defoliation of the host plant, the presumed start of pupation, or mortality.

Temperature. Air temperatures on evenings when searches were made ranged from 7.5°C to 28.5°C but larvae were never seen to emerge at temperatures less than 10°C. Ground temperatures adjacent to the ant and larvae refuge nests were about 1°C lower than air temperature. Rain also inhibited larval feeding.

Plant size. Generally the *B. spinosa* bushes were upright, single-stemmed and bushy; a few were multi-stemmed and lax, and some of the taller plants were bowed over to the extent that the upper part of the stem was parallel to the ground. The figures for height given in Table 1 are the length of the plant rather than the distance of its tip above ground level. This measure was used to give a better indication of the length of travel for a larva to reach the youngest foliage. *B. spinosa* hosts are log-normally distributed (Fig. 1) with

60% of the plants being less than 1 m in length and only 10% exceeding 1.5 m.

Overgrazing. When the number of larvae per plant was high, or the size of the plant was small, overgrazing occurred. In some instances bushes were totally defoliated and larvae, with attendant ants, were found wandering on bare branches. Regeneration would generally start to occur within a few weeks although some plants did not recover. Larvae did not persist with their nocturnal visits for long after the foliage had been completely grazed. It would seem that those which survived remained within the ants' nest until new leaves were available.

Bushes #G and #BB were contiguous and some of their branches were touching. On one occasion, prolonged exposure to bright torchlight caused a late instar larva on #BB to retreat down the trunk to a nest at its base. The two plants hosted

Bush	Height (mm)	Max. no. larvae
A	770	6
B	630	3
C	1650	6
D	1130	4
E	2000	1*
F	850	15
G	500	4
H	420	4
I	710	4
J	500	6
K	430	1
L	590	1
M	720	1
N	1230	1
O	950	1*
P	420	1
Q	1660	1
R	1140	4
S	760	1
T	1110	1*
U	850	2
V	1220	1*
W	1010	1*
X	1070	1*
Y	340	4
Z	530	3
AA	540	1
BB	600	3
CC	1360	2
Total		84

*Larvae present but not counted; attributed with '1' to give conservative colony total.

Table 1. Host plant height and larval numbers.

median	765 mm
mean	890 mm
std. dev.	419 mm
range	340 – 2000 mm
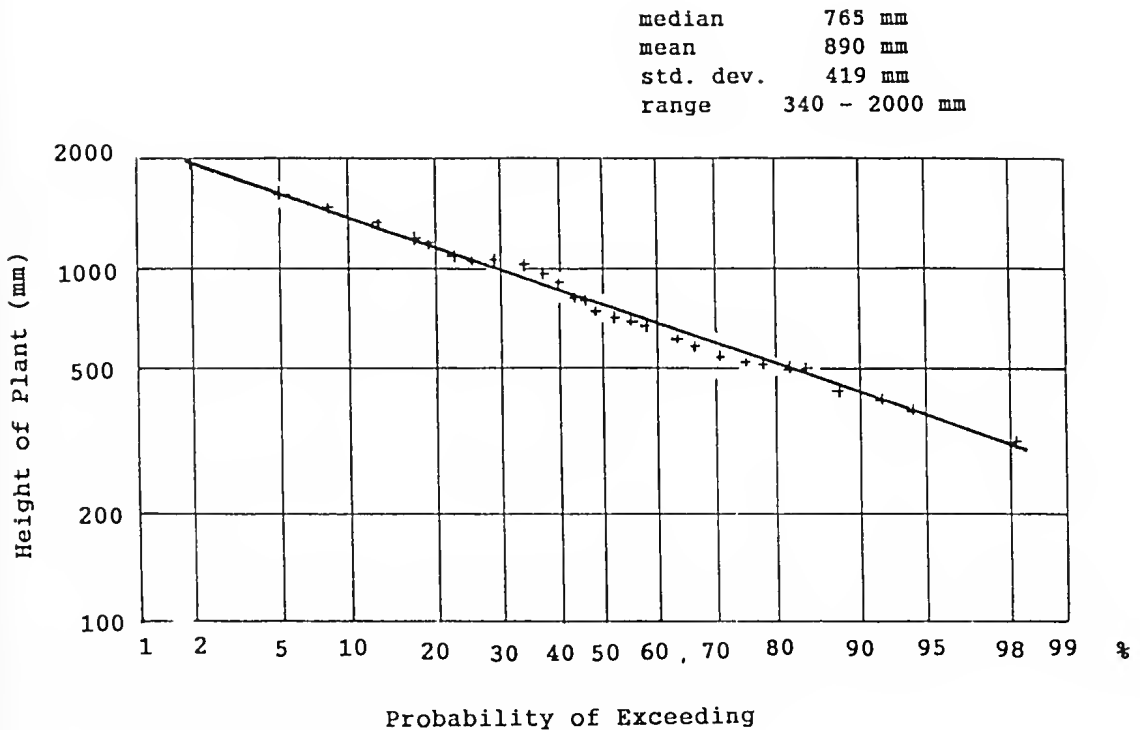
Fig. 1. Log-probability plot of host plant height.

separate populations but #BB had been defoliated while #G remained leafy throughout. This ease seems to suggest that the larvae stay loyal to their own bush and ant nest, even though alternative food may be readily available.

It would seem possible that defoliation of the host plant and the consequent enforced starvation of the larva could result in a delayed pupation. As a crude measure of the food available to each larva, the height of each bush was divided by the maximum number of larvae that it had supported. This number was plotted against the latest date on which caterpillars were seen on the bush, with the assumption that this represented the onset of pupation (Fig. 2). Whilst the points are broadly scattered there is a general trend towards a later pupation when there is a lower available food resource.

Instars. Four instars were regularly seen and recognised by eye according to size: 5-8 mm, 10-12 mm, 15-17 mm, and 19-22 mm, and the smallest has darker anal and thoraeic plates.

These probably correspond to the third and subsequent instars recognised by Braby (1990). Larvae which were first or second instar (ea. 3 mm) were found on 9 April, 25 April and 17 May; they were probably the progeny of late-flying adults.

Adults

Flight periods. The earliest adult to be seen in the eolony was a male on 19 December 1987 at 1155 hours (Eastern Summer Time) when the temperature was 18°C. There seemed to be four flight periods during the season with the peak of aetivity occurring from the 6-9 January (Fig 3).

Temperature. Sunlight and an adequate temperature seem to be a prerequisite for adults to become aetive in the colony. Fig. 4 shows that there is a tendency for earliest flight time to oceur later in the day if air temperatures are lower ($r = -0.33$, $n = 21$). On a typieal day aetivity commences about 1030 hours and is virtually over by 1600 hours. Late in the day when the site is in
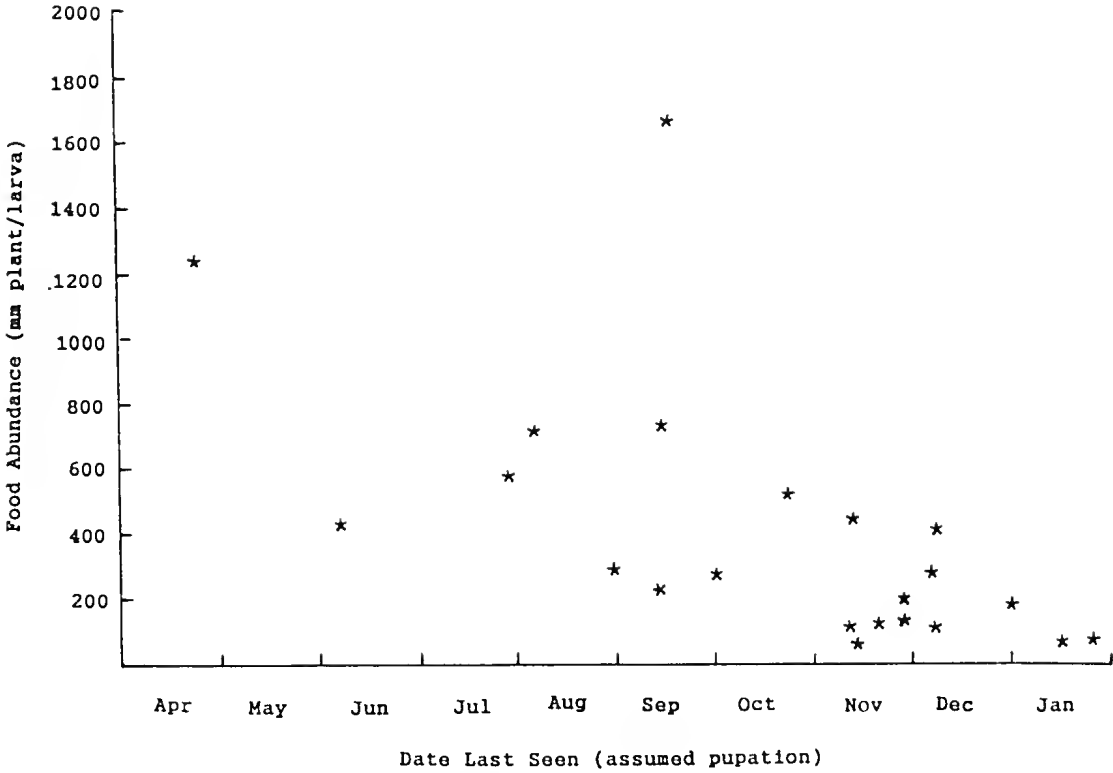
Fig. 2. Relationship of pupation date with food resource.
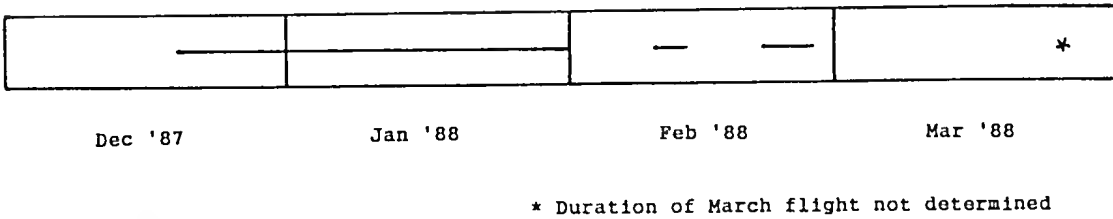
Fig. 3. Flight periods for adult *Paralucia pyrodiscus lucida*.

dappled shade the adults move to taller *Bursaria* plants on the edge of the colony where they are in full sunlight.

Flight patterns. The most obvious activities in the colony on a warm sunny day are adults either basking in the sunlight or performing a spectacular circling flight. Four different flight patterns were observed involving males: (a) slow fluttering; (b) 'exploratory'; (c) conspecific spiral; and (d) other spiral. More detailed descriptions are given in the Appendix.

Neither of the behaviours that consisted of a spiral flight with another insect included female *P. p. lucida*. Every instance appeared to be a male defending a territory against a conspecific or
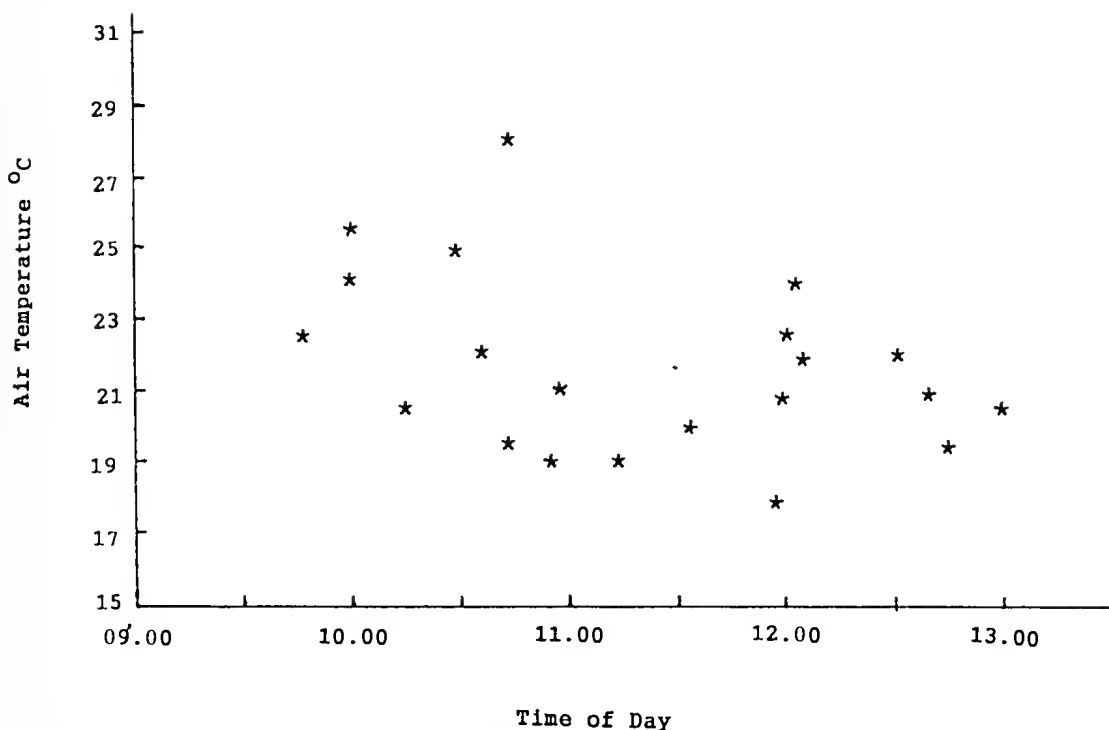
Fig. 4. Air temperature and start of flight activity.

another species that appeared to give the same stimulus or pose a threat. Female flight was similar to the male type (a) but usually closer to the ground.

Fifty-six flights of type (b), (c) or (d) were timed and the results are summarised in Table 2. Sometimes returning males were retriggered before perching, but on each occasion the additional flight time was very short and the total was within the range of the other observations. Exploratory flights of type (b) on average were shorter than those which involved a territorial element. The time spent away from the perch is significantly lower for type (b) exploratory flights than it is when the male is triggered by a conspecific (one-tailed t test, $P<0.05$) or with the pooled results for all butterfly triggers ($P<0.05$). Although it is not statistically significant, the average time spent 'investigating' another species is shorter than that required for a territorial defence. Territorial flights occurred more often than the other flight types.

Basking. When conditions were still and sunny, male and female adults basked with their backs facing the sun and wings opened. It was common

	No apparent trigger	Triggered by *P. p. lucida*	Triggered by other butterfly spp.
Number	13	28	15
Mean (sec.)	20.5	31.0	27.5
Std dev.	13.7	19.5	25.0
Range (sec.)	3–50	6–69	2–87

Table 2. Duration of exploratory or triggered flight by males.

to see a butterfly land, rotate its body so that the sun shone on it from behind, and then spread its wings to a dihedral angle of 120°. During a long basking period position was adjusted to track the movement of the sun. Wind, even a light breeze, was sufficient to cause basking butterflies to close their wings and show only the cryptically coloured undersides. Clouds passing across the face of the sun would also cause the butterflies to close their wings. However after a few minutes they would open them to about 30° dihedral angle and then a little later to 90°, returning to the open position

when the sun reappeared. The change in bright-ness seemed to cause the initial closing, not the absence of direct sunlight. On warm, but clouded days adults could sometimes be found basking with a full 120° wing opening oriented so that their dorsal surfaces would be normal to the direction from which the sun's rays would have come if there had been no cloud cover. The most common basking position was head up but adults perched on pendant branch tips sometimes assumed a head down position but still with their dorsal surface normal to the sun's direction. Occasion-ally a basking adult would rotate through ninety degrees and adjust its wing angle so that the sun would strike one wing normal to its surface.

Males and females, when in the 'wings closed' position, sometimes performed a display in which they slowly moved their wings alternatively in a scissors-like motion parallel to their body.

Mating. Newly emerged female *P. p. lucida* were first seen on 30 December 1987, eleven days after the first of the males had emerged. Only one attempted and one successful mating was observed. A female entered the colony and triggered a male to flight. They performed a close fluttering flight along the ground for a metre or so, and then landed with the male 20–30 mm behind the female, both facing in the same direction. The male started to quiver its partially opened wings very rapidly, perhaps to activate scent scales from what could be a black sex brand at the distal end of the ecll on its forewings. (The female lacks that marking.) After a few seconds of wing quivering the female flew with the male following but the male appeared to give up the chase after a few metres and returned to its original perch.

On a later occasion a small male mated tail to tail with a large female for four minutes and then took up a perch from which it spiralled with other overflying males. Nine minutes after the first mating had finished a second female arrived. The male landed just behind and fluttered its wings rapidly. It then moved into the tail to tail position and mated for 2 hours 18 minutes.

Egg laying. On 3 January 1988 a female was seen to lay two eggs on a food plant that was about 1200 mm high. No *Notoncus enormis* were present, nor did they appear later in the day or that night. On only one occasion were *Notoncus* ants found foraging in broad daylight, and that was on an early October morning. They usually emerged about half an hour before sunset. No sightings of the ants were ever made on plants that were not hosts to *P. p. lucida* larvae.

Of importance was the discovery of three eggs on the underside of a leaf on a small potted *Bursaria*, one of two that had been placed in the colony. This plant had never been seen to have *Notoncus* on it and there was no sign of a nest at its base. Five days later, in the early morning, one of the eggs was found to have disappeared; by late in the day they had all gone. No predator was found, but on another plant a lacewing larva of the genus *Chrysopa* seemed to be attempting to eat an egg. In the first week of February 1988 one of the potted plants had 3 hatched eggs on it and the other plant had 2 hatched and one unhatched eggs. These plants never did become larval hosts but adult females were obviously pre-pared to lay without the stimulus of an attendant ant.

Vagility. Occasional observations of butterflies away from the core of the colony are detailed in the Appendix.

Second generation

Sixty-four eggs were found on 13 plants, in 35 separate clusters (Table 3). Most of the eggs had been laid underneath leaves, but occasionally they were found on the trunk or a branch, on top of the leaf, or in the leaf axil. The first egg was found on 3 January; by 21 February, forty-one of the sixty-four had hatched, a 64% success rate.

The batch of six eggs was located on 15 January 1988 and one week later they had all hatched. Two larvae approximately 2 mm long were seen on the trunk and side branches about 0.3 m above the ground attended by palpating *N. enormis*. By 17 March there were four larvae about 10 mm long feeding on the plant, probably fourth instar.

Later in the season larvae were found on 16 plants: 10 used in the previous season and 6 new ones. One of the previous season's plants where eggs had been located had no larvae, and four of

Cluster size	Number	Total eggs
6	1	6
4	1	4
3	5	15
2	11	22
1	17	17
Total	35	64

Table 3.   Egg cluster size for second generation (64 eggs were found in 35 clusters).

| | Number of plants in second generation which were larval hosts: | | |
	in previous season	new for second season	Total
Egg batches located	5	8	13
of which hatching successful	4	2	6
Larvae present but eggs had not been located	6	4	10

Table 4. Location and hatching success of second generation egg batches.

the new season's plants that had eggs did not now reveal larvae. This is summarised in Table 4. The sample was small but it suggests that:

plants which were not hosts in the previous season tended to have a lower success rate than those which had been hosts;

in spite of the previous point, a substantial part of the colony can form on plants that were not previously hosts.

Other taxa

Observations of other invertebrates which have the potential to compete for the resources required by *P. p. lucida* or to become a predator are given in the Appendix.

DISCUSSION

Stunted plants and delayed pupation

Most authors who have discussed the larval biology of *P. p. lucida* have commented on the stunted form of its host plant (Braby 1990; Crosby 1987; Crosby et al. 1987; New 1987). Of the 29 bushes in the West Riding colony that contained larvae, 60% were less than one metre in height (Fig. 1). Because the larvae must travel from the ant nest at the base of the plant to the leaves to feed, there must be an optimal size that minimises the energy expended in travelling but provides sufficient biomass for the larva to reach maturity. The single observation that suggests plant fidelity, even though it may be completely grazed and alternatives are available, would place even greater pressure on optimal selection.

A miscalculation in selecting plant size, or the presence of a multiple egg brood, can lead to complete defoliation of the plant before larval development is complete. It appears that the caterpillars then remain quiescent in the ant nest until leaf regeneration occurs. This would enforce a delayed pupation and the data of Fig. 2, even though scattered, do suggest that pupation occurs later if there is a lower available food resource.

Cottrell (1984) quotes the example of *Maculinea arion* (Lycaenidae: Polyommatinae) larvae which are capable of starving for long periods and then of regaining size and resuming growth when food becomes available. At least in the colony under study, delayed pupation of some individuals is a more plausible explanation for the second wave of flying adults than Braby's (1990) bivoltine hypothesis. Braby's (1990) observation that adults of the second emergence are often notably smaller is consistent with a restricted food intake during the larval stage.

Myrmecophilous lycaenids suffer the nutritional nitrogen burden of meeting their own developmental requirements as well as secreting amino acids for attendant ants (Pierce 1985). Larvae of *Malacosoma americanum* (Lepidoptera: Lasiocampidae) preferred young leaves to mature ones in choice tests (Peterson 1987) and those fed on mature leaves alone showed lower pupal weight, poorer survival and less efficient growth. Cottrell (1984) noted that many lycaenids feed exclusively on plant parts that are especially rich in nitrogenous compounds such as new terminal shoots, buds and flowers. It might be a better strategy for a larva to await nitrogen rich regrowth on its original plant rather than transfer to another food plant of old growth even if it means a delayed ecdysis.

In comparing butterflies which lay eggs singly or in clusters, Stamp (1980) postulates that dispersed eggs may be advantageous for parasitoid and predator avoidance; single larvae are less likely to defoliate their host plant and have to find a new food source; or there is reduced competition for pupation sites. While she considered that it might be advantageous for female lycaenids to deposit eggs in clusters due to the larval association with ants her review of the literature found no apparent relationship between egg clustering and mutualism of caterpillars and ants. Kitching (1981), using wider sources, asserts that there is a strong association between egg clustering and myrmecophily among Australian lycaenids but refrains from speculating on the

nature of any causal relationship. However, in his sample, 35% of species laying eggs singly have an obligate myrmecophily and *P. p. lucida* should fall within this group as it lays singly or in small clusters (Table 3; Vaughan 1988). Laying single eggs or small batches is a practice consistent with a species that should optimise its host plant size.

A secondary consequence of heavy grazing, even to the extent of complete defoliation, on optimally sized bushes is that the plants will remain stunted and thus exhibit symptoms of poor health (New 1987) or, mistakenly, other debilitating causes (Crosby 1987). It is highly likely that it is grazing which keeps the larval hosts small, not phenotypic differences (contra Braby 1990; Vaughan 1987, 1988).

Basking behaviour and territoriality

The most obvious behaviour in an Eltham Copper colony on a sunny day is basking and vertical spiral flights involving two, or rarely more, butterflies.

Almost invariably a basking butterfly will sit with wings spread and normal to the sun's direction. Basking would appear to be a mechanism primarily for thermoregulation. Generally activity commences in the colony about 1030 hours and is virtually complete by 1600 hours. A species which basks from late morning to mid afternoon will naturally tend to face northwest and this is consistent with observations of site aspect by Crosby (1987), Crosby et al. (1987) and Vaughan (1987, 1988).

Scott (1974) categorises three mate-locating behaviours for butterflies: perching, patrolling and pheromones. He did not consider defense of a perching spot to be true territoriality because the location could drift as the day progressed or with changes in lighting or weather. Vertical encounters by perching species were seen as an attempt to determine the sex of the other participant. Arnold (1983) describes the behaviour of five lycaenids which fly out from their perches to investigate passing insects and generally return if the other is not a conspecific male (*Callophrys mossii, Plebejus icaroides, Euphilotes enoptes, E. battoides, Apodemia mormo*). *C. mossii* routinely investigates other males that enter its territory and the ensuing encounters are characterised by vertical flights. Certain perching sites are obviously preferred. In an experimental field study of *Pararge aegeria* (Lepidoptera : Satyridae) Davies (1978) determined that males competed for sunspots which gave sufficient warmth to enable them to remain active and they were the

best sites for locating females. Spiral flights were a territorial defense and the resident always won, irrespective of age or condition. They were not, as proposed by Scott (1974), a means to determine the sex of the other participant.

With *P. p. lucida* three flight types from a perch were observed: triggered by a conspecific male; triggered by another butterfly species; and flights with no obvious trigger, termed here 'exploratory'. Table 2 shows that exploratory flights were significantly shorter but there was no statistical difference between the two triggered flight types. No spiral flights from the colony under study involved a female (contra Vaughn 1988) so the behaviour noted is consistent with the defense of a perching site as in Davies' (1978) experiments. Distinctively marked or damaged resident male Eltham Coppers were seen to win contests and preferred perching sites did migrate with the movement of the sun.

Mate location

Other than Vaughan's (1988) misinterpretation of the male territorial flight as a courtship dance there is no published description of mate location and copulation for this species. Edwards & Common (1978) mention the flight of the congeneric *P. spinifera* as being close to ground near the foodplant and slower than the male. This is an apt description also for the flight of females at this site. However there are occasions when males make low, slow fluttering flights which cannot be distinguished by the human eye from the style of female flights. A male which sights the female from a perch and then approaches her must be responding to some visual or olfactory clue. Wing pattern dimorphism is slight and the different shape of female wings is possibly not distinguishable in flight. Obara (1970) demonstrated that the wings of *Pieris rapae* females reflected near ultraviolet radiation while those of males did not. Males detected females and models by this difference. It is feasible that *P. p. lucida* also uses a sex differentiation of this type and is worthy of an ultraviolet sensitive photographic study.

The wing quivering action of the male prior to mating is consistent with the release of pheromones from androconia. Scoble (1992) suggests that pheromones usually tend to inhibit female flight rather than stimulating them to mate. Some of the lycaenids studied by Arnold (1983) exhibit behaviour that could be interpreted in this way. Androconial scales are used by Eliot (1973) as one of the character states in his phylogenetic study

of the Lycaenidae. He places *Paralucia* in the tribe Luciini of the subfamily Theclinae and this group has 'primitive' androconia which barely differ from ordinary scales. Scales from the small black wing spot of male specimens are linear with multifid distal endings and do not appear to differ from other black wing scales. Female specimens in the collection of the Museum of Victoria do not have a corresponding black spot on the forewing (K. Walker, pers. comm.) so there appears to be some sexual dimorphism. Eliot (1973) includes diagrams of scent scales from the Lycaenidae which are entire and not plumose as in the typical belief about androconia, and so the scales from the previously unrecorded putative sex brand of *P. p. lucida* should not be dismissed as normal without further detailed investigation.

Host selection

The obligate relationship of the Eltham Copper butterfly with its foodplant (*B. spinosa*) and its attendant ant (*N. enormis*) raises a number of questions about host plant selection by the ovipositing female. Choosing the optimal size of foodplant is a related decision.

Sweet Bursaria must have some special property that causes the Eltham Copper to use it exclusively as a larval host. Because of the additional nutritional load necessary to produce ant attracting secretions, Pierce (1985) expects selection to favour ant-tended lycaenids which specialise on protein rich plants. It would be an informative study to see if *B. spinosa* exhibits any nitrogen enhancing adaptations such as those summarised by Bowen (1981): nodules; proteoid roots; cyanophyte or other mycorrhizal symbionts.

Brown (1955) described the ant species as being a nocturnal or crepuscular above-ground feeder and the observations of both Vaughan (1988) and myself (pers. obs.) support this for the local colonies. The presence of ants in daytime is not a cue for the female butterfly.

Other butterfly species have solved the mutualism problem by ovipositing in the presence of the appropriate ant or by another taxon (particularly Hemiptera) which also attracts the particular ant species (Atsatt 1981) but this does not seem to be the method employed by the Eltham Copper. Egg laying on potted plants that had never contained an ant nest supports the belief that ants or other taxa do not determine the oviposition site. According to Cottrell (1984) many tribes in the Theclinae oviposit directly onto plant surfaces utilising only cues that derive from the plant itself.

Vaughan (1988) noted that ant nests located beneath Sweet Bursaria at Eltham had few workers and no apparent brood but there was a major ant colony within the vicinity. He quotes similar observations by Keith Hately at Kiata.

The most parsimonious hypothesis is: adult females are able to detect the host plant and lay small egg clusters on appropriately sized bushes; nocturnal foraging ants locate eggs at random and then establish a temporary nest at the base of the plant to await larval hatching. This assumes that ants can identify *Paralucia* eggs through olfactory means but it does not address the relationship between the temporary nests and the main colony. There is no selective advantage in maintaining small cadres of worker ants remote from the breeding colony, so there must be some connection between the secretion collection sites and the main colony. Perhaps some main colony workers travel each night to the temporary nests to collect and transport lycaenid fluids by trophallaxis. Further observations and manipulative experiments to test these suppositions would be invaluable.

Vagility

Within 100 metres of the study site is a remnant Bursaria/Long Leaf Box Association that has been preserved within the housing development. It appears to be typical Eltham Copper habitat and possibly represents the vegetation that covered much of the land that had been cleared in the few years prior to this study. Despite numerous visits to the site during the season, no larvae or adults were found. This was neither source nor sink for adults of the local colony.

The greatest distance that adults were found from the centre of the colony was 40 metres and even this distance was a rare occurrence. If this is, indeed, a true measure of their vagility, the colony has possibly been isolated for at least twenty years with no apparent deterioration in its viability.

In his study of endangered American lycaenids Arnold (1983) noted that the strong correlation between the occurrence of adults and the presence of larval foodplants and nectar resources indicated the stringent microhabitat needs of each species. Also, mate location by rare species is optimised when the adults are aggregated whereas for common species there is no selective advantage in being clumped. These habitat and behavioural requirements appear to have selected for individuals with low vagility. The same conclusion can be reached for the local populations of the Eltham Copper.

CONCLUSIONS

Much of the anecdotal history of the Eltham
Copper Butterfly can be explained in terms of
the biology of the species. Its preference for
small food plants probably results from a strategy
which optimises the energy required for nightly
travel distance and adequate biomass to complete
development. The stunted or diseased appearance
of the bushes is generally due to overgrazing.

A second flight peak in each season is more
likely to be due to delayed pupation of individuals
which have been restricted to an under-sized food-
plant rather than to a second rapidly developing
generation.

Basking in late morning to mid afternoon is
facilitated by localities with a northwesterly aspect
and territorial defence of preferred sunny patches
as basking sites leads to spectacular spiral flights
between males.

Further studies on mate recognition, oviposition
cues, and the tripartite ecology of butterfly-plant-
ant would be of great value.

Because of the delayed pupation of some larvae
within the colony, due to overgrazing, they can
still be present when the next generation of eggs
is laid by early emerging adults. The management
implication of at least one stage always being
present on *Bursaria* plants is that suggestions of
slashing to keep the stature of bushes low and
therefore attractive to the butterfly (Vaughan 1988)
will result in the loss of some individuals, either
as egg or larva.

ACKNOWLEDGEMENTS

REFERENCES

ARNOLD, R. A., 1983. Ecological studies of six en-
dangered butterflies (Lepidoptera, Lycaenidae):
Island biogeography, patch dynamics and the
design of habitat preserves. *University of Cali-
fornia Publications in Entomology* 99: 1-161.
ATSATT, P. R., 1981. Ant-dependent food plant selec-
tion by the Mistletoe Butterfly *Ogyris amaryllis*
(Lycaenidae). *Oecologia* 48: 60-63.
BOWEN, G. D., 1981. Coping with Low Nutrients, in
The Biology of Australian Plants, J. S. Pate

& A.J. McComb, eds, University of Western
Australia Press.
BRABY, M. F., 1990. The life history and biology of
Paralucia pyrodiscus lucida Crosby (Lepidoptera:
Lycaenidae). *Journal of the Australian Entomo-
logical Society* 29: 41-50.
BROWN, W. L., 1955. A revision of the Australian ant
genus *Notoncus* Emery, with notes on the other
genera of Melophorini. *Bulletin of the Museum
of Comparative Zoology* 113: 474-494.
CALAFURI, F., 1987. Rare Butterfly is discovered again.
Diamond Valley News 31 March, p. 21.
COMMON, I. F. B. & WATERHOUSE, D. F., 1972. Butter-
flies of Australia. Angus & Robertson, Sydney.
COTTRELL, C. B., 1984. Aphytophagy in butterflies: its
relationship to myrmecophily. *Zoological Journal
of the Linnean Society* 79: 1-57.
CROSBY, D. F., 1951. A new geographical race of an
Australian butterfly. *Victorian Naturalist* 67:
225-227.
CROSBY, D. F., 1987. The Conservation status of the
Eltham Copper Butterfly (*Paralucia pyrodiscus
lucida* Crosby) (Lepidoptera Lycaenidae). *Arthur
Rylah Institute for Environmental Research Tech-
nical Report Series No. 81.*
CROSBY, D. F., NEW, T. R. & BRABY, M. F., 1987.
The Dull Copper Butterfly *Paralucia pyrodiscus*
(Rosenstock) (Lepidoptera: Lycaenidae). Supple-
ment to the Deputation to Honourable Joan
Kirner, Minister for Conservation, Forests and
Lands. 'Conservation of the Eltham Copper
Butterfly'. 25 March 1987.
DAVIES, N. B., 1978. Territorial defence in the Speckled
Wood Butterfly (*Pararge aegeria*): the resident
always wins. *Animal Behaviour* 26: 138-147.
EDWARDS, E. D. & COMMON, I. F. B., 1978. A new
species of *Paralucia* Waterhouse & Turner from
New South Wales. *Australian Entomological
Magazine* 5: 65-70.
ELIOT, J. N., 1973. The higher classification of the
Lycaenidae (Lepidoptera): a tentative arrange-
ment. *Bulletin of the British Museum (Natural
History) Entomology* 28: 373-505 + pls 1-6.
HINTON, H. E., 1949. Myrmecophilous Lycaenidae and
other Lepidoptera — a summary. *Proceedings of
the South London Entomological and Natural
History Society* 1949-1950: 111-175.
KITCHING, R. L., 1981. Egg clustering and the Southern
Hemisphere Lycaenids: comments on a paper by
N. E. Stamp. *American Naturalist* 118: 423-425.
MALICKY, H., 1970. New aspects on the association
between Lycaenid larvae (Lycaenidae) and ants
(Formicidae, Hymenoptera). *Journal of the
Lepidopterist's Society* 24: 190-202.
NEW, T. R., 1987. Butterfly Conservation. Entomo-
logical Society of Victoria.
OBARA, Y., 1970. Studies on the mating behaviour
of the White Cabbage Butterfly, *Pieris rapae
crucivora* Boisduval. III Near ultra-violet reflection
as the signal of intraspecific communication.
Zeitschrift für vergleichende Physiologie 69: 99-
116.

PETERSON, S. C., 1987. Communication of leaf suitability by gregarious eastern tent caterpillars (*Malacosoma americanum*). *Ecological Entomology* 12: 283–289.

PIERCE, N. E., 1985. Lycaenid butterflies and ants: selection for nitrogen-fixing and other protein-rich food plants. *American Naturalist* 125: 888–895.

SCOBLE, M. J., 1992. The Lepidoptera. British Museum (Natural History). Oxford University Press.

SCOTT, J. A., 1974. Mate locating behaviour of butterflies. *American Midland Naturalist* 91: 103–117.

STAMP, N. E., 1980. Egg deposition patterns in butterflies: why do some species cluster their eggs rather than deposit them singly? *American Naturalist* 115: 367–380.

VAUGHAN, P. J., 1987. The Eltham Copper Butterfly Draft Management Plan. *Arthur Rylah Institute for Environmental Research Technical Report Series No. 57.*

VAUGHAN, P. J., 1988. Management Plan for the Eltham Copper Butterfly (*Paralucia pyrodiscus lucida* Crosby) (Lepidoptera : Lycaenidae). *Arthur Rylah Institute for Environmental Research Technical Report Series No. 79.*

APPENDIX

Additional or more detailed observations than those presented in the main text:

Male flight patterns

Four flight patterns were recognised:

(a) a slow fluttering flight across the tops of the larval food plants and through the undergrowth, usually restricted to 0.5 to 2 m above the ground.

(b) a basking male will fly rapidly from his perch and return to the same spot within 20 seconds.

(c) a basking male will be triggered to flight by an overflying male. They spiral about each other rapidly and often rise to heights up to 10 m. Usually within 30 seconds one of the males will return to the original perch. On a number of occasions the male that had been triggered was sufficiently distinctive to be recognised as the one that resumed the perch site. This has all of the hallmarks of a territorial encounter. It was not unusual to see a third male join a spiralling pair.

(d) a basking male will be triggered by a species other than another *P. p. lucida* male. On most occasions the stimulus was the Common Brown butterfly (*Heteronympha merope merope*) but *Geitoneura acantha ocrea*, *Ocybadistes walkeri sothis*, and *Zizina otis labradus* also triggered the spiral flight. A wasp of unknown species, and a syrphid fly, did not evoke flight when they flew over a basking male at a distance that would be expected to cause a reaction if another butterfly had been involved.

Vagility

Almost all of the adult activity was confined to the area of the colony where larvae had been observed, or to a sunny site thickly covered with *Bursaria* bushes 1 to 2 m tall, about 5 m to the south. On five occasions adults were found further away:

a sleeping male roosting about 6 m northwest of the centre of the colony;

males performing a spiral dance 17 m northwest;

a male basking 23 m northwest;

females, on two occasions, basking about 40 m north of the colony.

Other taxa

Between late August and late September *N. enormis* were observed tending aphids on bushes which also hosted the butterfly larvae. In one instance two larvae were surrounded by aphids identified as *Macrosiphum euphorbiae* (Thomas) (G. Berg, pers. comm.). This is the Potato Aphid, a polyphagous species, probably present by coincidence.

During October a number of *B. spinosa* plants in the colony and in other local plots displayed a strong fasciation of the terminal leaves. In October 1995, Dr Laurence Mound (Natural History Museum, London) examined specimens of thrips from the colony's *Bursaria* galls and found them to be *Neocecidothrips bursariae*.

Another minor and indirect food competitor was a psyllid from the subfamily Spondyliaspinae. They were discovered as spent husks adorning the backs of their predator, a lacewing larva (*Chrysopa* sp.). They pose no threat to the butterfly colony.

It is often surmised that the *P. p. lucida* larvae attract the ants with secretions from their dorsal and dorsolateral organs in return for protection from predators and parasites (Hinton

1949; Malicky 1970). On one occasion two ants were seen to shepherd a 3 mm larva along the trunk and beneath the arched leg of an *Olios* *diana*. The spider flinched its leg as the ants passed as though it had been bitten; it then sidled a short way around the trunk.

STUDIES ON WESTERN AUSTRALIAN PERMIAN BRACHIOPODS 12. ADDITIONS TO THE LATE ASSELIAN–TASTUBIAN FAUNAS

N. W. ARCHBOLD

School of Aquatic Science and Natural Resources Management, Deakin University, Rusden Campus, 662 Blackburn Road, Clayton, Victoria 3168

New species and records of Early Permian (Asselian–Tastubian) brachiopods from the Lyons Group and Carrandibby Formation of the Carnarvon Basin, and the Grant Group of the Canning Basin, that are important for the geology and stratigraphy including the biostratigraphy of the Early Permian of Western Australia, are described and illustrated. New taxa described are *Neochonetes (Sommeriella) obrieni* sp. nov., *Etherilosia carolynae* sp. nov., *Etherilosia calytrixi* sp. nov. and *Rhynchopora australasica* sp. nov. The age of the earliest Permian faunas of Western Australia is briefly discussed with the conclusion that they possibly range in age from Asselian to Late Tastubian.

BRACHIOPODS are abundant throughout the Permian-marine sequences of the Perth, Carnarvon and Canning Basins of Western Australia, where they are valuable for zonation purposes and inter-basinal correlation (Archbold 1993a; Archbold et al. 1993). Despite numerous recent studies on the brachiopod faunas having been published (e.g. Archbold 1993b), the earliest Permian (Asselian–Tastubian) faunas of Western Australia remain only partially described. The present study brings together new collections and specimens from the Grant Group of the Canning Basin and the Lyons Group and Carrandibby Formation of the Carnarvon Basin and revises material from the subsurface Grant Group previously partially described by Waterhouse (in Foster & Waterhouse 1988).

References to the Permian stratigraphy of the Carnarvon and Canning Basins are provided in previous parts of this series although recent work is indicated in this study as are additional remarks on the age and correlation of pertinent faunas. Specific locality and stratigraphical data are also provided below.

All illustrated material is deposited in either the collections of the Geological Survey of Western Australia, Perth (GSWA F) or the Commonwealth Palaeontological Collection (CPC) of the Australian Geological Survey Organisation, Canberra (AGSO).

All illustrated specimens of new species, other than holotypes, are paratypes.

STRATIGRAPHY, LOCALITIES AND AGE

Canning Basin

A small brachiopod assemblage from the Wye Worry Member of the Carolyn Formation, Grant Group (see Crowe & Towner 1981), discovered by geologists of the Australian Geological Survey Organisation, was sent to the present author for study by Dr P. E. O'Brien. Previously discovered marine fossils from this unit were molluscan dominated (Diekins et al. 1978). The present assemblage, consisting of *Neochonetes (Sommeriella) obrieni* sp. nov., *Etherilosia carolynae* sp. nov., *Costatumulus* sp. *Trigonotreta* sp. and fragments of *Deltopecten* sp. was discovered on the Noonkanbah 1:250 000 map sheet (Crowe & Towner 1981) at latitude 18°42'48"S and longitude 124°54'48"E, east of Mount Tuckfield and east of the Carolyn Bore. A stratigraphical section of the locality after a sketch section provided by Dr O'Brien, is given in Fig. 1. The correlation of these assemblages from the Wye Worry Member is most likely with the faunas of the Upper Lyons Group and Carrandibby Formation of the Carnarvon Basin (Archbold 1993a), an interpretation strengthened by the discovery of a specimen of *Neochonetes (Sommeriella) obrieni* sp. nov. from the Carrandibby Formation (see below).

The brachiopod assemblage described by Waterhouse (in Foster & Waterhouse 1988) from an isolated subsurface section within the Grant Group on the Barbwire Terrace is revised and fully
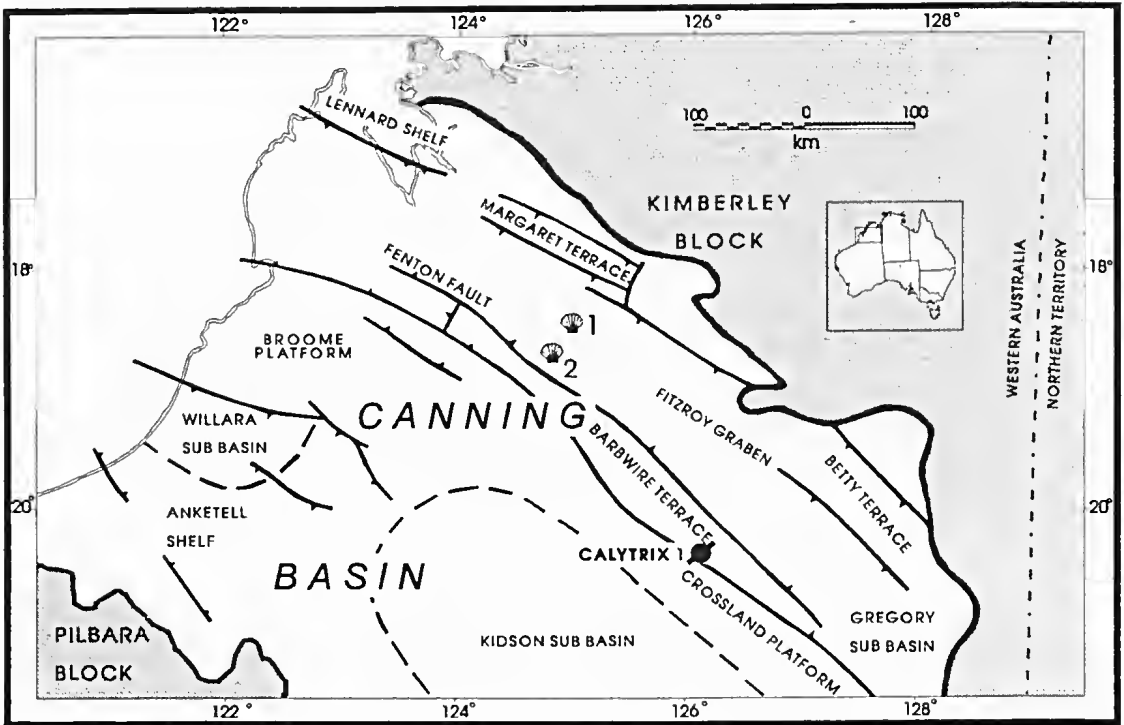
Fig. 1.   Locality map of Grant Group marine fossil localities.   1 = Dickins et al. (1978) locality.   2 = new faunal locality described herein.

illustrated in this study. Details of the stratigraphy of the core section are provided by Foster & Waterhouse (1988) and comprehensive sedimentologieal data is provided by Redfern (1991) who defined three subsurface formations being in ascending order the Hoya, Calytrix and Clianthus formations. The marine fossils described by Waterhouse (in Foster & Waterhouse 1988) are from the Calytrix Formation. Redfern & Millward (1994) concluded that the Barbwire Terrace Formations represented only the upper part of the Grant Group, a view shown by Jones & Young (1993: 15) who correlated the Calytrix Formation with the Wye Worry Member of the Carolyn Formation.

Briggs (1991: 34) initially correlated the upper Grant Group (Carolyn Formation) with the Callytharra Formation of the Carnarvon Basin. He subsequently (1993: 52) correlated the Calytrix fauna with that of the underlying Carrandibby Formation, a view also indicated by Archbold (1993a), but Briggs preferred an early Tastubian age for the assemblage. Briggs (1993: 54) argued that the age of the Callytharra Formation was late

Tastubian and that its age had 'been distorted by the correlation of earlier workers' by correlation with 'the younger (Sterlitamakian) Nura Nura Member (Canning Basin)'. While there is always scope for interpretation in correlating faunas, in this case the following points are noteworthy. *Metalegoceras* sp. nov. from the base of the Callytharra Formation is considered to be Sterlitamakian in age (Glenister et al. 1993: 292). Comparable metalegoceratids indicate correlation of the Nura Nura Member (Canning Basin), Callytharra Formation and Fossil Cliff Member (Perth Basin) and a Sterlitamakian age is indicated (Glenister et al. 1993: 56). Discussions on the age of *Svetlanoceras irwinense* are equivocal (cf. Briggs 1993: 54–55 and Glenister et al. 1993: 56). Data from brachiopods and other groups indicate significant faunal links between the Fossil Cliff Member, Callytharra Formation and the Nura Nura Member (and equivalent units) for correlation purposes (Thomas & Diekins 1954; Dickins 1963; Archbold 1988, 1990, 1993a) and hence a Sterlitamakian age is retained for these units in this study. As a result, the age of the Carrandibby Formation, immediately

underlying the Callytharra Formation and the Upper Grant Group are regarded as being late Tastubian in age as in Archbold (1993a).

The brachiopod assemblage from the Calytrix Formation includes the following forms as revised in this study: *?Streptorhynchus* spp., *Arctitreta* sp., *Neochonetes (Sommeriella) obrieni* sp. nov., *Etherilosia calytrixi* sp. nov., *Costatumulus capillatus* (Waterhouse), *?Cyrtella* sp., *Trigonotreta* sp., *?Martinia* sp. and *Spiriferellina* sp. The use of

Ripple & parallel bedded fine sandstone

← Flooding surface

Well Bedded medium sandstone

← Base of Poole Sandstone

Fine Sandstone and silty mudstone

Massive to parallel laminated medium sandstone

Obscured

Massive to poorly bedded diamictite

Fine sandstone with clay rich layers and marine fossils

Obscured

Massive medium sandstone

10 m

Fig. 2. Measured section cropping out east of Carolyn Bore (latitude 18°42'48"S; longitude 124°54'48"E) Noonkanbah 1:250 000 sheet.

latex for making casts from natural moulds has been invaluable in elucidating details not described by Waterhouse (in Foster & Waterhouse 1988) and all forms are illustrated herein. The age of the assemblage is considered to be late Tastubian.

Carnarvon Basin

Additional material is described from two outcrop localities within the Lyons Group and from the base of the Lyons Group and the Carrandibby Formation from the BMR 8, Mount Madeline Core (see Mercer 1967 for details of this well). Locality GSWA 30111, described as Lyons Group cropping out near Snake Well, Eudamullah Station, Carnarvon Basin has yielded, in addition to the *Linoproductus* sp. recorded by Archbold (1983, fig. 1A, 1B), incomplete specimens of *Taeniothaerus* sp., *?Callytharrella* sp. and *Spiriferella* sp. which are placed on record in this study. These specimens are the oldest record of these genera in the Western Australian Permian and may provide a record of a brief interglacial period during the glacially dominated Lyons Group period of sedimentation. The lithology of the samples is that of a silty fine sandstone with no shell material perserved and hence is unlike the preservation of fossils in the overlying Callytharra Formation.

From the stratigraphically lowest known marine locality in the Lyons Group (AGSO locality ML6, 5.6 km west of north of Moogooree Homestead), *Rhynchopora australasica* sp. nov. is described. Specimens are also described and figured from Core 32 of the Mount Madeline (BMR 8) well, Lyons Group, Carnarvon Basin from a depth of 2994–3004 feet (=912.5–915.5 metres) from Core 18 of the same well (depth 1665–1671 feet = 507.5–509.3 metres) a specimen of *Neochonetes (Sommeriella) obrieni* sp. nov. is recorded and illustrated. This core interval represents a limestone at the base of the Carrandibby Formation (Mercer 1967).

Rhynchopora australasica sp. nov. occurs low in the *Lyonia lyoni* Zone (Archbold 1993a) and is probably of Asselian age. Other faunal elements outlined above are of Late Tastubian age and appear to equate with the *Trigonotreta occidentalis* Zone (Archbold 1993a).

Palynological data

Foster (in Foster & Waterhouse 1988), on the basis of palynofloras retrieved from the Calytrix No. 1 bore core, established the *Granulatisporites confluens* Oppel-zone. This Oppel-zone, found throughout the three formations defined by
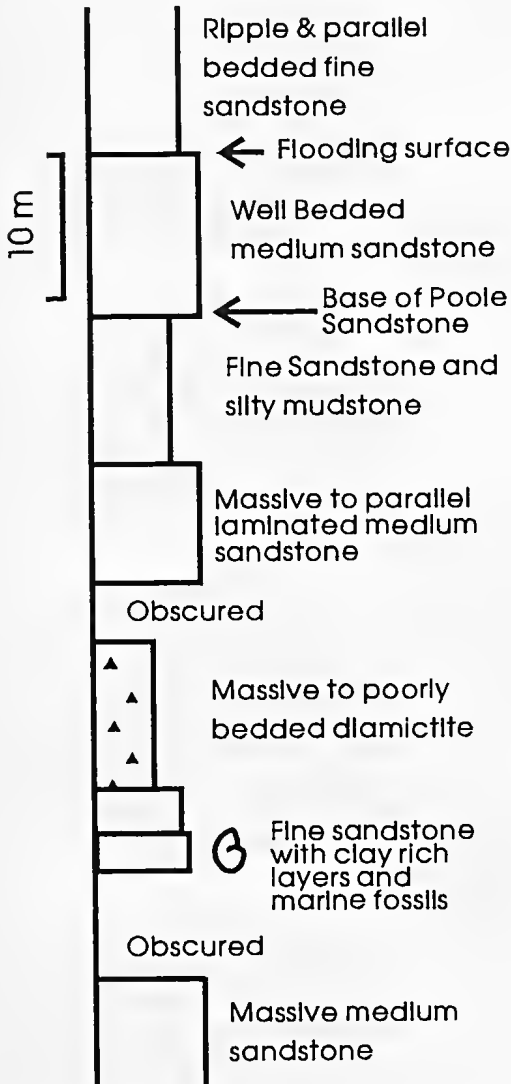
Redfern (1991), occurs stratigraphically below Stage 3a palynofloras which are themselves marked by the entry of *Pseudoreticulatispora pseudoreticulata,* as reviewed by Foster (in Burger et al. 1992). Backhouse (1991, 1993) has argued that the *Granulatisporites confluens* Oppel-zone represents the upper part of the underlying Stage 2 palynofloral unit. The present author would argue on the basis of the data from marine faunas and superpositional stratigraphy, that the *Granulatisporites confluens* Oppel-zone is of Tastubian age, ranging down into the Asselian.

SYSTEMATIC PALAEONTOLOGY

Phylum BRACHIOPODA

Order STROPHOMENIDA Öpik, 1934

Suborder ORTHOTETIDINA Waagen, 1884

Superfamily ORTHOTETOIDEA Waagen, 1884

Family STREPTORHYNCHIDAE Stehli, 1954

Genus **Streptorhynchus** King, 1850

Type species.   Terebratulites pelargonatus Schlotheim, 1816.

?Streptorhynchus spp.

Fig. 5A–B

Comments. Two illustrated specimens (GSWA F49444–49445) of dorsal valves indicate the presence of *Streptorhynchus* or an allied genus in the assemblage from the Calytrix Formation, Grant Group. A small external mould (GSWA F49444, maximum width 8.8 mm) possesses fine, bifurcating costellae (9 per 5 mm at anterior margin). An incomplete dorsal valve internal mould (GSWA F49445, estimated maximum width 25 + mm) possesses the characteristic dorsal cardinalia of *Streptorhynchus.* The specimens are inadequate for comparison with other Western Australian species.

Genus **Arctitreta** Whitfield, 1908

Type species.   Arctitreta pearyi Whitfield, 1908.

Arctitreta sp.

Fig. 5C

Comments. A damaged dorsal valve from the Calytrix Formation, Grant Group, (GSWA F49446, maximum width 23 mm, length 24.5 mm, hinge width 19 + mm) strongly recalls *Arctitreta plicatilis* (Hosking 1932; see also Thomas 1958a and Archbold et al. 1993) from the Callytharra Formation, in details of valve size and costellae. The valve is thick-walled. The specimen represents the oldest occurrence of the genus from the marine Permian of Western Australia.

Order CHONETIDA Nalivkin, 1979

Suborder CHONETIDINA Muir-Wood, 1955

Superfamily CHONETOIDEA Bronn, 1862

Family RUGOSOCHONETIDAE Muir-Wood, 1962

Subfamily RUGOSOCHONETINAE Muir-Wood, 1962

Genus **Neochonetes** Muir-Wood, 1962

Subgenus **Neochonetes (Sommeriella)** Archbold, 1982

Type Species.   Chonetes prattii Davidson, 1859.

Neochonetes (Sommeriella) obrieni sp. nov.

Figs 3A–N, 5D–I, 8B

Neochonetes (Sommeriella) aff. *pratti.* — Waterhouse (in Foster & Waterhouse) 1988: 155, fig. 7a, b.
Neochonetes (Sommeriella) aff. *prattii.* — Archbold & Dickins 1991: 4.
Neochonetes (Sommeriella) sp. nov.. — Archbold 1993a: 314, 315.

Fig. 3.   *Neochonetes (Sommeriella) obrieni* sp. nov. All specimens from Wye Worry Member, Carolyn Formation, Grant Group. A–C, Holotype, CPC 33501, ventral valve in postero-ventral, ventral and antero-ventral views, ×2.6. D, E, CPC 33502, ventral valve internal mould in postero-ventral and posterior views, ×2.5. F, CPC 33503, dorsal valve, interior view, ×2.5. G, CPC 33504, shell in dorsal view, ×2.6. H, CPC 33505, internal mould of ventral valve, ×2.5. I, CPC 33506, worn dorsal valve interior, ×3.8. J, CPC 33507, ventral valve in ventral view, ×2.5. K, CPC 33508, dorsal valve external view, ×2.5. L, CPC 33509, dorsal valve internal mould, ×2.5. M, CPC 33510, worn dorsal valve in dorsal view, ×2.5. N, CPC 33511, shell in dorsal view, ×2.6.
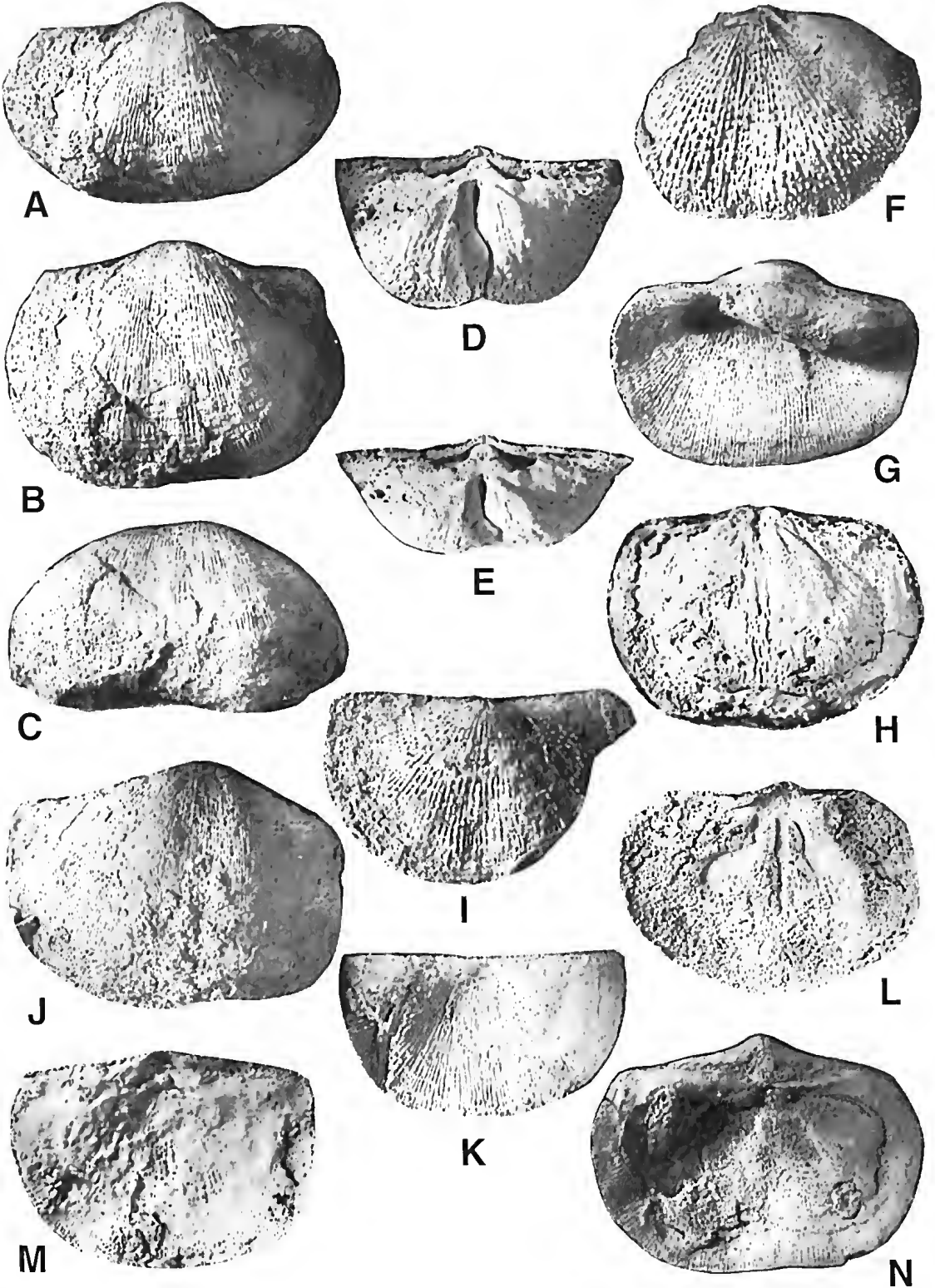
Etymology.   For Dr Philip E. O'Brien.

Holotype. CPC 33501, a ventral valve (illustrated fig. 3A–C) from east of the Carolyn Bore, Wye Worry Member, Carolyn Formation, Grant Group.

Other figure material. CPC 33512, a ventral valve from Mount Madeline 8 Bore Core, Carrandibby Formation, Carnarvon Basin. CPC 33502–33511, 1 ventral valve, 2 internal moulds of ventral valves, 5 dorsal valves and 2 shells from east of the Carolyn Bore, Wye Worry Member, Carolyn Formation, Grant Group, Canning Basin GSWA F47187, a ventral valve, GSWA F47186, an external mould of the dorsal surface of a shell, GSWA F49447, a ventral valve external mould and GSWA F49448, a decorticated ventral valve, all from the Calytrix Formation, Grant Group, Canning Basin.

Measurements (in mm).   e = estimate.

Specimen	Hinge width	Maximum width	Ventral height	Dorsal height
CPC 33501	16.0	19.3	13.5	–
CPC 33512	11.8	13.5e	10.5	–
CPC 33502	16.8	17.0	–	–
CPC 33503	–	17.4e	–	11.8
CPC 33504	–	16.9	12.4	11.6
CPC 33505	16.6	19.6	13.8	–
CPC 33506	11.2	11.8e	–	7.6
CPC 33507	–	21.8	17.2	–
CPC 33508	17.0	17.4	–	10.4
CPC 33509	–	19.2	–	12.6
CPC 33510	15.0	15.6	–	10.1
CPC 33511	15.2	17.9	13.0	11.6
GSWA F47187	–	12.4	9.0	–
GSWA F47186	17.4	18.0e	10.2	8.6
GSWA F49447	–	12.0e	7.1	–
GSWA F49448	–	21.2e	15.0e	

Description.   Small to medium sized *Neochonetes.* Convexity of ventral valve moderate with median flattening rather than distinct sulcus. Dorsal valve gently concave with no median fold. Greatest shell width at about mid-length of shell. Exterior shell surface with weakly developed growth lines and fine capillae (4 to 5 per mm at 10 mm from umbones) increasing in number by bifurcation. Ventral interarea low, dorsal interarea very low. Cardinal spines project at variable angle (30° to 50° on available material). Ventral umbo low, rounded.

Ventral interior with short, stout teeth. Median septum arises under delthyrium, thickened, about half valve length. Muscle scars strongly impressed. Diductor scars large, coarsely striated. Lateral and anterior margins strongly papillose.

Cardinal process low, poorly known. Chilidium unknown. Alveolus distinct. Median septum distinct, broad, approximately 60% of valve length.

Brachial ridges distinct at maturity. Anterior of valve papillose. Submature interior with papillose radiating ridges.

Discussion.   N. (S.) obrieni sp. nov. is a distinctive small to medium sized representative of the genus readily distinguished from other species by means of its lack of sulcus, smaller size and moderately convex ventral valve at maturity. *N. (S.) prattii* (Davidson) as revised by Archbold (1981d), *N. (S.) tenuicapillatus* Archbold (1981d) and *N. (S.) cockbaini* Archbold (in Archbold & Shi 1993) are all large species with distinct sulci of younger (Sterlitamakian–Artinskian) ages from Western Australia. The small *Neochonetes (S.) hockingi* Archbold (1991a) from the Aktastinian Wooramel Group, Carnarvon Basin, Western Australia possesses coarser capillae and a less convex ventral valve than *N. (S.) obrieni* sp. nov. *N. (S.) robustus* Archbold (1981d) from the early Baigendzhinian of Western Australia is a strongly convex species with a rounded outline at maturity.

Order PRODUCTIDA
Sarycheva & Sokolskaya, 1959

Suborder STROPHALOSIIDINA
Waterhouse, 1975

Superfamily STROPHALOSIOIDEA
Schuchert, 1913

Family STROPHALOSIIDAE Schuchert, 1913

Subfamily STROPHALOSIINAE
Schuchert, 1913

Genus **Etherilosia** Archbold, 1993

Type species.   Strophalosia etheridgei Prendergast, 1943.

Comments.   The distinctive spine arrangement of the ventral valve including rhizoid spines and the large cicatrix of attachment described for *Etherilosia* by Archbold (1993b) indicates that the genus is appropriately accorded full generic rank rather than a subgenus of *Heteralosia.*

Etherilosia carolynae sp. nov.

Fig. 4A–I

Heteralosia sp. nov. Archbold 1993a: 315.

Etymology.   After the Carolyn Valley, Saint Georges Range, Canning Basin.

Holotype.   CPC 33513, an external mould of a ventral valve, from east of the Carolyn Bore, Wye Worry Member, Carolyn Formation, Grant Group.
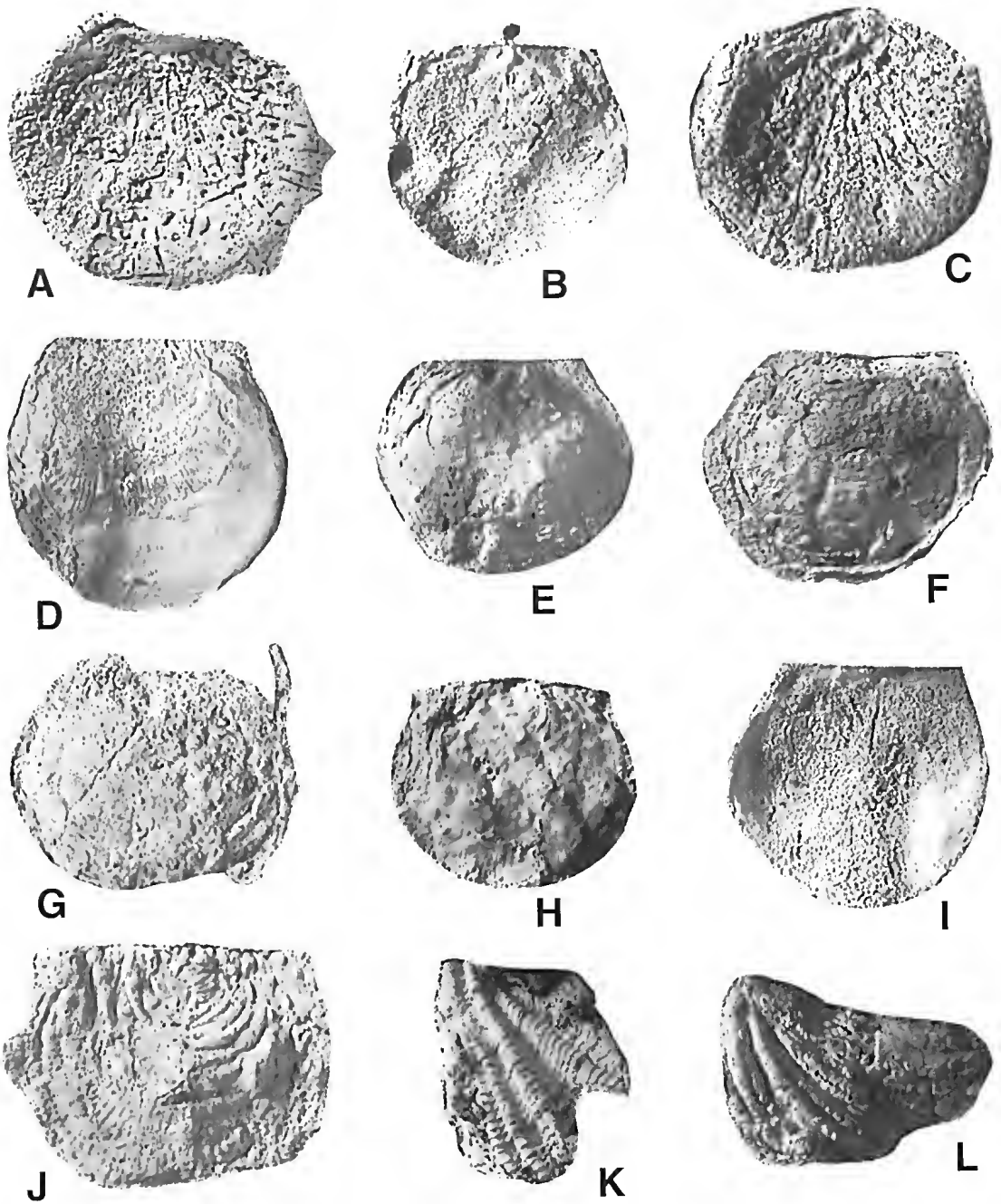
Fig. 4. All specimens from Wye Worry Member, Carolyn Formation, Grant Group.   A–I, *Etherilosia carolynae* sp. nov.   A, holotype, CPC 33513, external mould of ventral valve, ×3.   B, CPC 33514, dorsal valve internal mould, ×3.   C, CPC 33515, ventral valve external mould, ×4.   D, I, CPC 33516, dorsal valve external mould, and internal mould, ×3.2.   E, CPC 33517, worn dorsal valve, internal view, ×3.   F, CPC 33518, dorsal valve external mould, ×3.2.   G, CPC 33519, dorsal valve external mould with mould of ventral rhizoid spine, ×4.2. H, CPC 33520, worn dorsal valve, internal view, ×3.2.   J, *Costatumulus* sp., CPC 33521, dorsal valve external mould, ×5.5.   K, L, *Trigonotreta* sp.   K, CPC 33522, incomplete ventral valve exterior, ×3.5.   L, CPC 33523, incomplete ventral valve exterior, ×2.5.

Other figured material. CPC 33514–33520, 1 ventral valve external mould, 2 dorsal valve internal moulds, 5 dorsal valve external moulds all from east of the Carolyn Bore, Wye Worry Member, Carolyn Formation, Grant Group.

Measurements (in mm). e = estimate.

Specimen	Hinge width	Maximum width	Ventral height	Dorsal height
CPC 33513	—	15.0	13.8	—
CPC 33514	9.0	11.5	—	10.5
CPC 33515	7.4	9.0	8.8	7.8
CPC 33516	9.6	12.2	—	11.8
CPC 33517	9.0	12.1	—	10.4
CPC 33519	5.4	8.0	—	6.2
CPC 33520	7.2e	10.2e	—	9.6

Description. Shell medium sized for genus, subcircular to transverse in outline. Hinge extremities finely pointed at maturity. Ears small, variably developed. Ventral valve moderately convex. Cicatrix poorly known but of moderate size. Ventral valve spinose with spines in poorly developed concentric rows, adherent posterior, suberect anteriorly at maturity. Spines spaced at 1 to 2 mm intervals, individual spines from 0.3 mm to 0.5 mm thick. Rhizoid spines apparently present as indicated by CPC 33519.

Interareas distinct, flat, relatively low. Delthyrium small, pseudodeltidium unknown.

Dorsal valve flat during early ontogeny, concave anteriorly, weakly developed geniculation in front of visceral disc. Concentric lamellae distinct, fine capillae prominent (3 to 4 per mm). Spines absent.

Ventral interior unknown. Cardinal process spike-like, interior face bilobed. Sockets small, moderately deep. Median septum thin, blade-like, approximately one-third valve length. Muscle scars and brachial ridges poorly developed.

Discussion. Finer ventral spines, lower ventral convexity, larger size at maturity and strongly developed capillae at submaturity and maturity

distinguish the new species from *Etherilosia etheridgei* (Prendergast 1943), sec Archbold (1986, fig. 3A–Z, AA–BB). *Etherilosia prendergastae* (Coleman 1957) as revised by Archbold (1986, 1993b), is of comparable size to *Etherilosia carolynae* sp. nov. and possesses relatively fine ventral spines but shows greater concavo-convexity. *Etherilosia calytrixi* sp. nov., as presently understood, is a smaller species with only a trace of fine capillae developed at the extreme anterior of the dorsal valve.

Etherilosia calytrixi sp. nov.

Fig. 5J–Q

Strophalosia cf. *subcircularis* — Waterhouse (in Foster & Waterhouse) 1988: 155, figs 7e, 8a–e.
small *Strophalosia* (partim) — Waterhouse 1989: 367.
Strophalosia cf. *irwinensis* — Archbold (in Archbold & Dickins) 1991: 4.
cf. *Strophalosia concentrica* — Briggs 1993: 52.
Heteralosia sp. nov. Archbold 1993a: 315.

Holotype. GSWA F47189, external mould of dorsal surface of shell from the Calytrix Formation, Grant Group, Canning Basin (figured by Waterhouse, in Foster & Waterhouse 1988, p. 156, fig 8a; refigured herein fig. 5L, M).

Other figured material. Two ventral valve external moulds (GSWA F47188, F49449); two ventral valve internal moulds (GSWA F47191, F49450); incomplete dorsal external mould, of shell (GSWA F47190), all from the Calytrix Formation, Grant Group, Canning Basin.

Measurements (in mm). e = estimate.

Specimen	Hinge width	Maximum width	Ventral height	Dorsal height
GSWA F47189	4.3	5.5	6.5	5.5
GSWA F47188	—	12.4	10.5+	—
GSWA F49449	—	12.5	10.0+	—
GSWA F47191	—	9.8e	11.1	—
GSWA F49450	—	10.1	9.5+	—
GSWA F47190	6.2e	8.0e	—	—

Fig 5. All specimens from Calytrix Formation, Grant Group. A, B, *?Streptorhynchus* sp. A, GSWA F49444, dorsal valve external mould, ×3.2. B, GSWA F49445, dorsal valve internal mould, ×1.2. C, *Arctitreta* sp. GSWA F49446, dorsal valve, external view, ×2.4. D–1, *Neochonetes (Sommeriella) obrieni* sp. nov. D, GSWA F49447, external mould of ventral valve, ×3.2. E, GSWA F49448, decorticated ventral valve, ventral view, ×2.5. F, G, GSWA 47187, ventral valve exterior and external mould of same valve, ×3.5. H, 1, GSWA F47186, external mould of dorsal shell surface and latex east of surface, ×3.5. J–Q, *Etherilosia calytrixi* sp. nov. J, GSWA F49449, latex east of ventral exterior, ×3.2. K, GSWA F49450, ventral valve internal mould, ×3. L, M, holotype, GSWA F47189, external mould of dorsal shell surface and latex east of surface, ×4.5. N, GSWA F47191, internal mould of ventral valve, ×3.2. O, GSWA F47190, incomplete dorsal external mould, ×4.2. P, Q, GSWA F47188, external mould of ventral valve and latex east of valve, ×3.2.
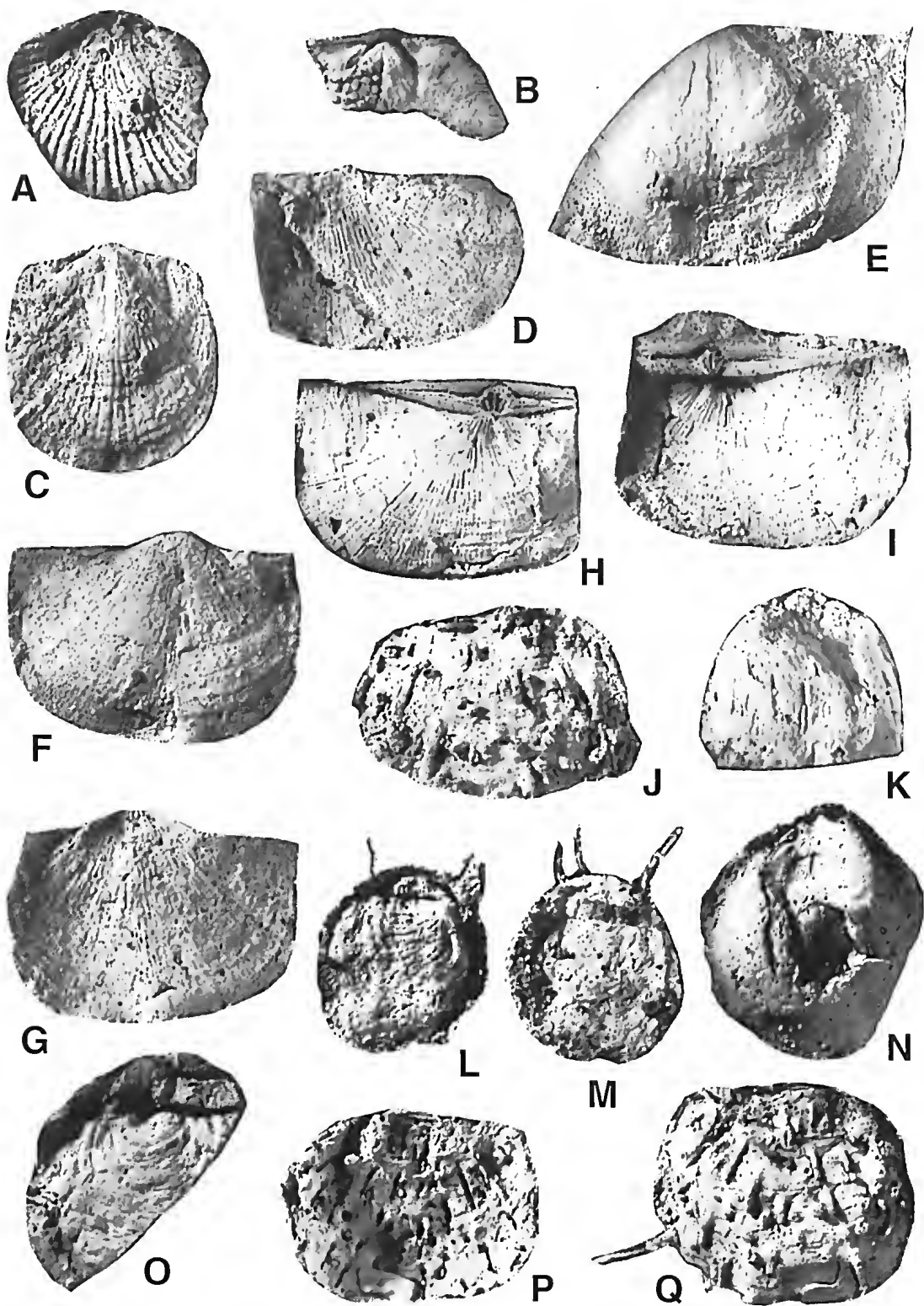
Description. Shell small for genus, circular to weakly transverse in outline. Hinge extremities weakly pointed, ears poorly developed. Ventral valve moderately to strongly convex, dorsal valve relatively flat. No ventral sulcus or dorsal fold. Maximum width close to mid-length. Cicatrix poorly known but apparently of moderate size judging from rhizoid spine impressions on GSWA F47189. Ventral valve spinose with spines of rhizoid type near umbo and sub-erect type over valve remainder. Body spines from 0.4 mm to 0.7 mm in diameter, 1.2 mm to 2 mm between spines. Spines arranged in poorly defined rows.

Interareas distinct, flat, relatively low, dorsal interarea at right angles to commissure on GSWA F47190. Pseudodeltidium distinct, narrow.

Dorsal spines absent, growth increments and traces of radial capillae weakly developed, the latter only anteriorly on GSWA F47190. Nepionic part of dorsal valve 2.2 mm wide and convex. Dorsal interior unknown.

Ventral interior with adductor scars on low, raised platform, diductor indistinct, rounded. Valve interior pustulose with anterior and lateral spines opening into valve.

Discussion. Considerable debate has surrounded the identity of these small specimens as indicated by the synonymy above. Most comparisons have been with much larger species of *Strophalosia* such as the Tasmanian species *Strophalosia concentrica* or *Strophalosia subcircularis*, both fully described and illustrated by Clarke (1970a, 1990, 1992), or the Western Australian species *Strophalosia irwinensis* Coleman (1957) as described by Archbold (1986). A re-examination of available material and the use of latex casts has revealed that the species is assignable to *Etherilosia* on the basis of its small size, moderate ventral convexity and ventral spine pattern including rhizoid spines not documented in the original description.

Etherilosia calytrixi sp. nov. is distinguished from *Etherilosia carolynae* sp. nov. by its smaller size, lack of prominent capillae and more strongly developed ventral convexity. *Etherilosia etheridgei* (Prendergast 1943), see Archbold (1986, fig. 3A–Z, AA–BB), is usually a small species with widely scattered ventral spines and a distinctly concave dorsal valve.

Suborder PRODUCTIDINA Waagen, 1883

Superfamily AULOSTEGOIDEA
Muir-Wood & Cooper, 1960

Family AULOSTEGIDAE
Muir-Wood & Cooper, 1960

Subfamily AULOSTEGINAE
Muir-Wood & Cooper, 1960

Genus **Taeniothaerus** Whitehouse, 1928

Type species. *Productus subquadratus* Morris, 1845.

Taeniothaerus sp.

Fig. 8A, C

Comments. Two incomplete specimens of ventral valves (a natural east and an external mould – GSWA F49462, F49463) provide the first record of *Taeniothaerus* from the Lyons Group of the Carnarvon Basin. The specimens from near Snake Well, Eudamullah Station, show the characteristic ventral spine pattern of the genus. Spine bases are of variable length on GSWA F49462, being 5 to 8 mm in length and spaced at 2.5 mm at the anterior of the specimen. The coarseness of the spine bases is unlike the much finer ventral spine bases of other Early Permian species of *Taeniothaerus* from Western Australia (Archbold et al. 1993). However, *Taeniothaerus aifamensis* Archbold (1991b, fig. 3F–I) from the Sterlitmakian (or perhaps Tastubian) of Irian Jaya possesses spines bases of comparable size although more tightly arranged. Eastern Australian Artinskian species of *Taeniothaerus* (see Parfrey 1983; Parfrey 1989; Briggs, in Waterhouse 1986b) are also characterised by relatively coarse ventral spines.

Superfamily PRODUCTOIDEA Gray, 1840

Family DICTYOCLOSTIDAE Stehi, 1954

Genus Callytharrella Archbold, 1985

Type species. *Dictyoclostus callytharrensis* Pendergast, 1943.

Callytharrella sp.

Fig. 8D

Comments. A single, incomplete, external mould of a dorsal valve (GSWA F49464) from near Snake Well, Eudamullah Station, Carnarvon Basin, is the first verified record of a reticulate productid from the Lyons Group. The specimen (estimated width = 30 mm, estimated height = 18 mm) is referred to *Callytharrella* and indicates a smaller species than *C. callytharrensis* (Prendergast) with significant geniculation of the dorsal valve at 16 mm from the umbo. Costae and rugae are comparable with those of *C. callytharrensis* but the dorsal fold is very weakly developed.
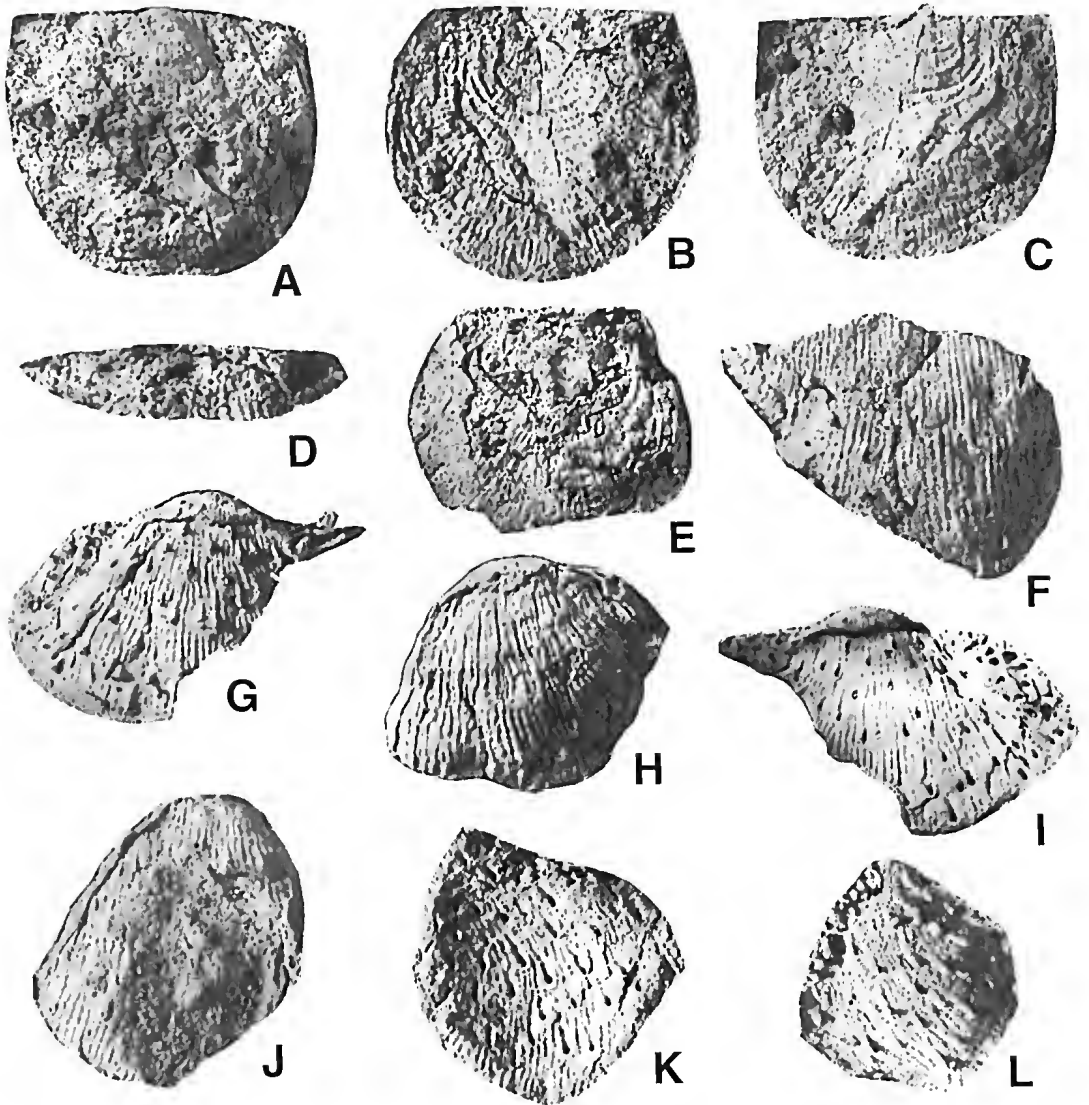
Fig. 6. All specimens from Calytrix Formation, Grant Group. A–L, *Costatumulus capillatus* (Waterhouse, 1988). A, D, GSWA F47194, dorsal valve external mould, full and anterior views, ×3. B, C, GSWA F47196, dorsal interior mould and latex cast of dorsal interior, ×3. E, GSWA F49451, dorsal valve external mould, ×3. F, GSWA F49452, latex east from incomplete ventral valve external mould, ×3.5. G, I, GSWA F47195, latex east and ventral valve external mould, ×3. H, GSWA F47192, internal mould of ventral valve, counterpart of GSWA F47195, ×3. J, GSWA F49453, latex east of ventral valve external mould, ×3. K, L, GSWA F47193, holotype, incomplete ventral valve external mould, ×3, and latex east, ×2.5.

Superfamily LINOPRODUCTOIDEA
Stehli, 1954

Family LINOPRODUCTIDAE Stehli, 1954

Subfamily AURICULISPININAE
Waterhouse, 1986b

Genus **Costatumulus** Waterhouse, 1983a

Type species. *Auriculispina tumida* Waterhouse, in Waterhouse et al. 1983.

Costatumulus capillatus (Waterhouse, 1988)

Fig. 6A–L

Terrakea capillata Waterhouse (in Foster & Waterhouse 1988), 156, fig. 8d–h.
Costatumulus capillata—Archbold 1993a, 315.

Holotype. A fragment of a ventral valve external mould (GSWA F47193) from the Calytrix Formation, Grant Group, Canning Basin (figured by Waterhouse, in Foster and Waterhouse 1988, p. 156, fig. 8e; refigured herein Fig. 6K, L).

Other figured material. Two dorsal valve external moulds (GSWA F47194, F49451); a dorsal valve internal mould (GSWA F47196); three incomplete ventral valve external moulds (GSWA F47195, F49452, F49453); a ventral valve internal mould (GSWA F47192) which is the internal mould of GSWA F47195).

Comments. This species was described in some detail by Waterhouse (in Foster and Waterhouse 1988) but the use of latex casts and additional specimens, as illustrated herein, permit the revision of morphological details and a reassessment of the generic position of the species. Ventral spines arise from spine bases of variable length which in turn arise from thickening of individual costellae. Preservation shows that ventral spines are hollow with delicate tubes of sediment being preserved on external moulds. Dorsal spines reported on the anterior of specimen GSWA F47194 by Waterhouse are not spines because the few small holes on the anterior margin of the external mould lack any central infilling sediment tubes which are to be expected from this type of preservation of productid spines. Furthermore the position of the holes would indicate that such spines arose between costellae rather than from them, again unlikely for a productoid brachiopod. Numerous fine hair like broken pieces of bryozoans are preserved with the dorsal external mould, GSWA F47194, are of various angles to the shell surface and the features previously interpreted as spine bases appear to be fragments of these. A second dorsal valve

external mould, GSWA F49451, possesses no trace of dorsal spines.

Additional specimens of ventral valve external moulds indicate that ventral spines are less numerous on the anterior trails of mature specimens.

This species is notable for its small size. Morphological features indicate that it is better assigned to *Costatumulus* but its small size is highly distinctive within the genus. *Terrakea* Booker (1930) is not yet reliably known from the Western Australian Permian (cf. Archbold 1993b).

Costatumulus sp.

Fig. 4J

Comments. A single specimen (CPC 33521) of a small dorsal valve from east of the Carolyn Bore, Wye Worry Member, Carolyn Formation, Grant Group indicates the presence of *Costatumulus* or a related genus. The specimen (7.8 mm wide, 6.5 mm length) lacks spines but possesses fine radial costellae and concentric rugae. Material is inadequate for comparison with other, larger, Western Australian species of the genus (Archbold 1993b).

Order SPIRIFERIDA Waagen, 1883

Suborder SPIRIFERIDINA Waagen, 1883

Superfamily SYRINGOTHYRIDOIDEA
Frederiks, 1926

Family SYRINGOTHYRIDIDAE
Frederiks, 1926

Subfamily PERMOSYRINXINAE
Waterhouse, 1986

Genus **Cyrtella** Frederiks, 1924

Type species. *Cyrtia kulikiana* Frederiks, 1916.

?Cyrtella sp.

Fig. 7A

Comments. A single specimen (GSWA F49454, estimated width 45 mm) of a ventral valve internal mould with a distinctive pointed muscle field, possible traces of punctae and divergent adminicula may represent a juvenile cyrtellid. It is figured for completeness of illustrating the fauna from the Calytrix Formation but is inadequate for comparison with other Western Australian cyrtellids.

Superfamily SPIRIFEROIDEA King, 1846

Family TRIGONOTRETIDAE Schuchert, 1893

Subfamily TRIGONOTRETINAE
Schuchert, 1893

Genus **Trigonotreta** Koenig, 1825

Type species.   *Trigonotreta stokesii* Koenig, 1825.

Trigonotreta spp.

Figs 4K, L, 7B–F

Figured material.   Two incomplete ventral valves (CPC 33522–33523) from east of the Carolyn Bore, Wye Worry Member, Carolyn Formation, Grant Group, Canning Basin. Two dorsal valve internal moulds (GSWA F49457–F49456), one ventral valve internal mould (GSWA F49455) and one ventral valve external mould (GSWA F49458) from the Calytrix Formation, Grant Group.

Measurements (in mm).   e = estimate.

Specimen	Hinge width	Maximum width	Ventral height	Dorsal height
CPC 33523	—	30.0e	—	—
GSWA F49457	15.0	18.0	—	9.5
GSWA F49456	—	24.0e	—	13.0+
GSWA F49455	35.0e	38.0e	17.0+	—
GSWA F49458	33.0	33.0	15.0+	—

Comments.   These specimens indicate the presence of *Trigonotreta* within the Tastubian faunas of the Canning Basin. Characteristic coarse primary costae with secondary bifurcations resulting in fascicles of three costae are developed on the larger specimens. While the specimens are inadequate for precise comparison with described early Permian *Trigonotreta* species from western and eastern Australia (Archbold & Thomas 1986; Archbold 1991a; Clarke 1990), they add to the Gondwanan record of the genus.
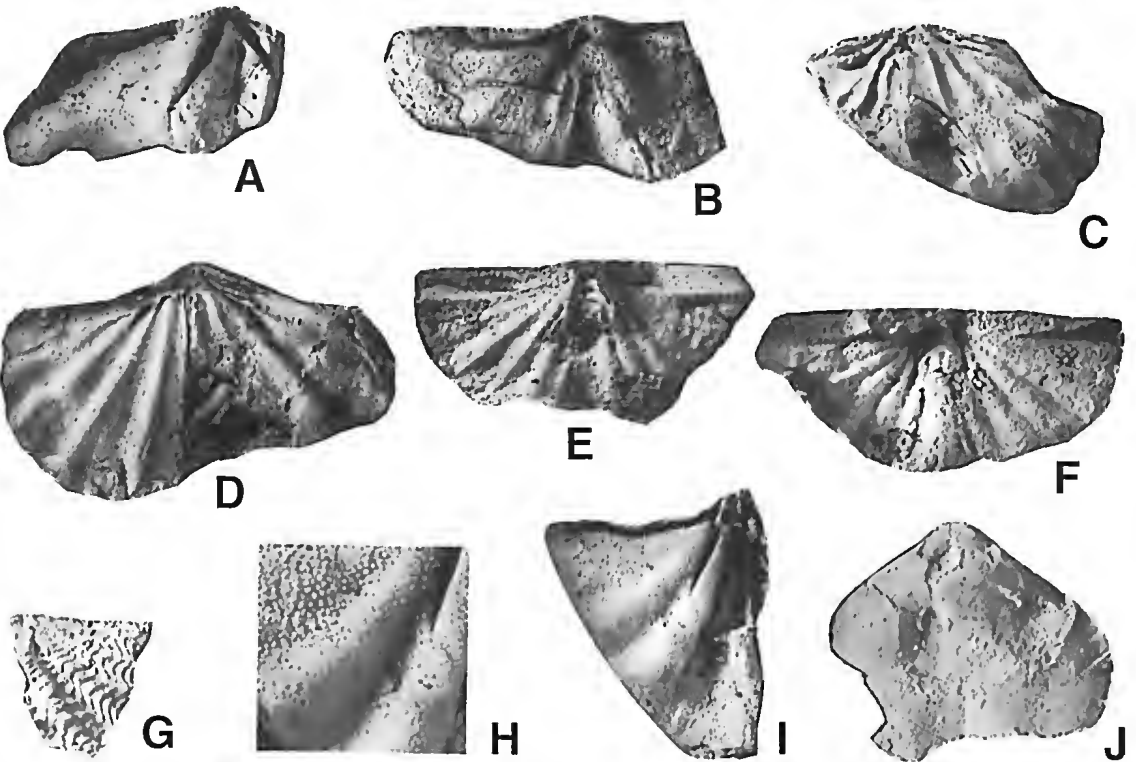
Fig. 7.   All specimens from Calytrix Formation, Grant Group.   A, GSWA F49454, *?Cyrtella* sp., ventral valve internal mould, ×1.5.   B–F, *Trigonotreta* spp.   B, GSWA F49455, ventral valve internal mould, ×1.4.   C, GSWA F49456, dorsal valve internal mould, ×1.8.   D, GSWA F49457, dorsal valve internal mould, ×2.5.   E, F, GSWA F49458, latex cast of ventral exterior and ventral valve external mould, ×1.2.   G–I, *Spiriferellina* sp.   G, GSWA F49459, latex cast of incomplete ventral valve external mould, ×3.   H, I, GSWA F49460, detail of ventral internal mould and internal mould, ×6 and ×2.6.   J, *?Martinia* sp. GSWA F49461, ventral valve in ventral view, ×2.6.

Subfamily SPIRIFERELLINAE
Waterhouse, 1968

Genus **Spiriferella** Tschernyschew, 1902

Type species. *Spirifer suranae* de Verneuil, in Murchison et al. 1845.

Spiriferella sp.

Fig. 8E

Comments. A single incomplete internal mould of a dorsal valve (GSWA F49465) from the Lyons Group near Snake Well, Eudamullah Station, Carnarvon Basin, possesses the characteristic coarse costae and elongated outline of a spiriferellinid. The valve is distinct from the Sterlitamakian *Elivina hoskingae* Archbold & Thomas (1985a), the dorsal valve of which possesses fine costae that bifurcate early in ontogeny. This specimen is the oldest record of a spiriferellinid from the Western Australian Permian.

Superfamily MARTINIOIDEA Waagen, 1883

Family MARTINIIDAE Waagen, 1883

Subfamily MARTINIINAE Waagen, 1883

Genus **Martinia** McCoy, 1844

Type species. *Spirifer glaber* Sowerby, 1820.

?Martinia sp.

Fig. 7J

Comments. A single, finely pustulose ventral valve (GSWA F49461), width 12 mm, length 10 mm, probably indicates the presence of *Martinia*, or an allied genus, in the fauna of the Calytrix Formation. Martiniids are not otherwise recorded

from the Western Australian Permian (Thomas 1969) — rather surprisingly given their cosmopolitan distribution during the early Permian.

Order SPIRIFERINIDA Ivanova 1972

Family CRENISPIRIFERIDAE
Cooper & Grant 1976a

Genus **Spiriferellina** Frederiks 1924

Type species. *Terebratulites cristatus* von Schlotheim 1816.

Spiriferellina sp.

Fig. 7G–I

Comments. An incomplete, thickly punctate ventral valve internal mould (GSWA F49460) and an incomplete, strongly lamellose, external mould of a ventral valve (GSWA F49459) from the Calytrix Formation, Grant Group, add to the minor record of spiriferinids from the Western Australian Permian (Archbold et al. 1993). The specimens are figured for completeness of the fauna and are tentatively referred to *Spiriferellina* Frederiks (1924).

Order RHYNCHONELLIDA Kühn 1949

Superfamily RHYNCHOPOROIDEA
Muir-Wood 1955

Family RHYNCHOPORIDAE Muir-Wood 1955

Genus **Rhynchopora** King 1865

Type species. *Terebratula geinitziana* de Verneuil, in Murchison et al. 1845.

Comments. The type species of *Rhynchopora* has been comprehensively studied by Erlanger (1981)

Fig. 8. All specimens from Lyons Group, Carnarvon Basin except for B from Carrandibby Formation, Carnarvon Basin. A, C, *Taeniothaerus* sp. A, GSWA F49462, natural cast of ventral exterior, ×1.5. C, GSWA F49463, external mould of juvenile ventral valve, ×1.5. B, *Neochonetes (Sommeriella) obrieni* sp. nov., CPC 33512, decorticated ventral valve in ventral view, ×3.2. D, *Callytharrella* sp., GSWA F49464, dorsal valve external mould, ×1.5. E, *Spiriferella* sp., GSWA F49465, dorsal valve internal mould, ×1.5. F–R, *Rhynchopora australasica* sp. nov. F, CPC 33532, incomplete ventral valve, ×1.6. G, CPC 33533, incomplete ventral valve, ×1.6. H, CPC 33529, latex cast of crushed ventral valve, ×1.5. I, CPC 33530, internal mould of dorsal valve, ×2. J, CPC 33534, ventral valve, ×1.6. K, CPC 33531, crushed internal mould of shell in dorsal view, ×2. L, CPC 33536, incomplete dorsal valve, ×1.8. M, CPC 33535, incomplete ventral valve, ×1.8. N, CPC 33524, holotype, ventral valve in ventral view, ×2.2. O, CPC 33525, ventral valve in ventral view, ×2. P, CPC 33527, incomplete ventral valve, ×2. Q, CPC 33526, worn ventral valve in ventral view, ×2. R, CPC 33528, worn ventral valve in ventral view, ×2.
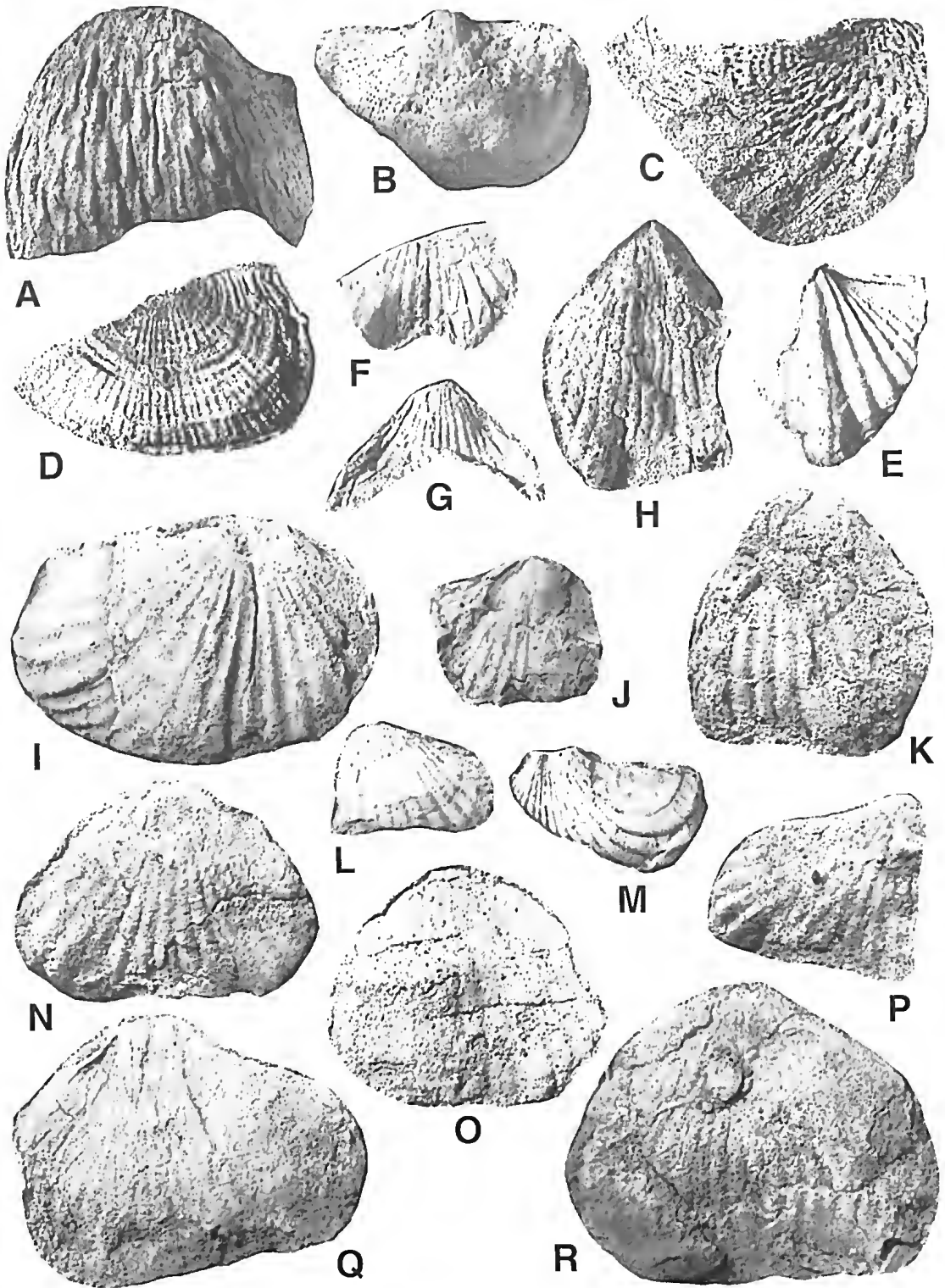
on the basis of topotypic material from the Kazanian Stage of Archangel Province, European Russia.

Rhynchopora australasica sp. nov.

Fig. 8F–R

Rhynchonellacea gen. ind. Dickins & Thomas 1959, 74, 77.
Rhychonellacean (*sic*) brachiopod Dickins 1967, 16.
Rhynchopora sp. nov. Thomas 1969, 218, 220, 228.
Rhynchopora Archbold et al. 1993, 45.
Rhynchopora sp. Archbold 1993a, 314.

Holotype. CPC 33524, a worn ventral valve from AGSO locality ML6, lowest known marine horizon of Lyons Group, 5.6 km west of north of Moogooree Homestead, Carnarvon Basin.

Other figured material. CPC 33525–33528, four ventral valves; CPC 33529 an external mould of a ventral valve; CPC 33530, an internal mould of a dorsal valve and CPC 33531, a distorted internal mould of a shell, all from AGSO locality ML6. CPC 33532–33535, four incomplete ventral valves and CPC 33536, an incomplete dorsal valve from Core 32 of the Mount Madeline (BMR 8) well, Lyons Group (depth in well 912.5–915.5 metres).

Measurements (in mm).   e = estimate.

Specimen	Maximum width	Ventral height	Dorsal height
CPC 33524	21.0	16.0	—
CPC 33525	22.0+	18.5	—
CPC 33526	27.5	22.0	—
CPC 33528	27.0	22.5	—
CPC 33530	26.0+	—	19.0+

Description. Large size for genus, subtriangular to rounded in outline. Ventral umbo with foramen. Maximum width at anterior of mid-length. Ventral sulcus arises 6 to 8 mm from ventral umbo, widens at wide angle (45–50°). Ventral costae arise at umbo, 5 to 6 pairs in sulcus, 4 to 6 pairs on lateral flanks. Costae initially fine and sharply rounded, by anterior of larger valves costae somewhat flattened with narrow interspaces. Costae up to 2 mm wide at anterior of valve.

Dorsal valve with 4 to 5 costae on each flank of fold with up to 6 costae on each lateral flank. Fold flattens at anterior of large specimens.

Punctae coarse — up to 8 or 10 per 2 mm anteriorly.

Ventral dental plates distinct, diverge at 25–30°. Dorsal median septum distinct. Other internal structures unknown.

Discussion. This distinctive, large species is moderately close to *Rhynchopora culta* Water-house (1982b) from the Tastubian faunas of Peninsular Thailand, which is a smaller species usually with a more trigonal outline and more inflated shell. Puntae are finer in the Thai species than *R. australasica* sp. nov.

R. culta reported from the Sterlitamakian of western Malaysia (see Shi & Waterhouse 1991, fig. 3 – 3,4) is a strongly inflated shell with coarser costae than those of *R. australasica* sp. nov.

Thomas (1969, p. 228) compared the new species with *R. lobjaensis* (sic) Tolmachev as figured by Likharev, (1934a) and Ustritsky & Chernyak (1963). Tolmachev's species *R. lobiensis* (see Tolmachev 1912, pl. 4, fig. 6; Tolmatschow 1915, pl. 4, fig. 6), has usually been misspelt as *lobjaensis* by subsequent authors (Likharev 1934a; Zavodovsky & Stepanov 1971; Abramov & Grigoryeva 1988) except for Likharev (1932) and Erlanger (1981). *R. lobiensis* is a large species from the Late Permian of the Kolyma–Omolan region of north-eastern Siberia, the Verkhoyansk Mountains and the Taimyr Peninsular (see Likharev 1934a, pl. 9, figs 12–24; Zavodovsky & Stepanov 1971, pl. 67, figs 7–10; Abramov & Grigoryeva 1988, pl. 16, figs 4, 6–9; Ustritsky & Chernyak 1963, pl. 27, figs 1–6). It is morphologically close to *R. australasica* sp. nov. in terms of size and outline but possesses widely divergent dental plates and a narrower ventral sulcus.

REFERENCES

References are supplementary to those in Parts 1–11 (*Proceedings of the Royal Society of Victoria*, vol. 91: 181; vol. 93: 109; vol. 95: 237; vol. 96: 83; vol. 97: 19; vol. 98: 97; vol. 99: 19; vol. 100: 21; vol. 102: 1; vol. 103: 55; vol. 105: 1).

ARCHBOLD, N. W., 1991a. Sudies on Western Australian Permian brachiopods 10. Faunas from the Wooramel Group, Carnarvon Basin. *Proceedings of the Royal Society of Victoria* 103: 55–66.

ARCHBOLD, N. W., 1991b. Late Paleozoic brachiopod faunas from Irian Jaya, Indonesia. In *Brachiopods through Time*, D. I. MacKinnon, D. E. Lee & J. D. Campbell, eds, A. A. Balkema, Rotterdam, 347–353.

ARCHBOLD, N. W., 1993a. A zonation of the Permian brachiopod faunas of western Australia. In *Gondwana Eight, Assembly, evolution and dispersal*, R. H. Findlay, R. Unrug, M. R. Banks & J. J. Veevers, eds, A. A. Balkema, Rotterdam, 313–321.

ARCHBOLD, N. W., 1993b. Studies on Western Australian Permian brachiopods 11. New genera, species and records. *Proceedings of the Royal Society of Victoria* 105: 1–29.

ARCHBOLD, N. W. & DICKINS, J. M., 1991. Australian Phanerozoic Timescales 6. Permian. A standard for the Permian System in Australia. *Bureau of Mineral Resources, Geology and Geophysics, Record* 1989/36: 1–17.

ARCHBOLD, N. W. & SHI, G. R., 1993. Aktastinian (Early Artinskian, Early Permian) brachiopods from the Jimba Calcarenite, Wooramel Group, Carnarvon Basin, Western Australia. *Proceedings of the Royal Society of Victoria* 105: 187–202.

ARCHBOLD, N. W., THOMAS, G. A. & SKWARKO, S. K., 1993. Brachiopods. *Bulletin of the Geological Survey of Western Australia* 136: 45–51, 196–264 + microfiche supplement.

BACKHOUSE, J., 1991. Permian palynostratigraphy of the Collie Basin, Western Australia. *Revue of Palaeobotany and Palynology* 67: 237–314.

BACKHOUSE, J., 1993. Palynology and correlation of Permian sediments in the Perth, Collie and Officer Basins, Western Australia. *Report of the Geological Survey of Western Australia* 34: 111–128.

BRIGGS, D. J. C., 1991. Correlation charts for the Permian of the Sydney–Bowen Basin and New England Orogen. *Twenty Fifth Newcastle Symposium on 'Advances in the Study of the Sydney Basin'*, Department of Geology, University of Newcastle, Newcastle, 30–37.

BRIGGS, D. J. C., 1993. Chronostratigraphic correlation of Australian Permian depositional sequences. *Twenty Seventh Newcastle Symposium on 'Advances in the Study of the Sydney Basin'*, Department of Geology, University of Newcastle, Newcastle, 51–58.

BURGER, D., FOSTER, C. B. & MCKELLAR, J. T., 1992. A review of Permian to Cretaceous palynostratigraphy in eastern Australia. *Bureau of Mineral Resources, Geology and Geophysics, Record* 1992/5: 1–26.

CLARKE, M. J., 1992. Hellyerian and Tamarian (Late Carboniferous–Lower Permian) invertebrate faunas from Tasmania. *Bulletin of the Geological Survey of Tasmania* 69: 1–52.

COOPER, G. A. & GRANT, R. E., 1976a. Permian brachiopods of West Texas, V. *Smithsonian Contributions to Paleobiology* 24: 2609–3159.

CROWE, R. W. A. & TOWNER, R. R., 1981. *1:250 000 Geological Series—Explanatory Notes. Noonkanbah, Western Australia, Sheet SE/51-12 International Index*. Australian Government Publishing Service, Canberra, 51 pp.

DICKINS, J. M., 1967. Permian macrofossils from Bores BMR 8 and BMR 9. *Report of the Bureau of Mineral Resources, Geology and Geophysics* 108: 14–19.

DICKINS, J. M. & THOMAS, G. A., 1959. The marine fauna of the Lyons Group and the Carrandibby Formation of the Carnarvon Basin, Western Australia. *Report of the Bureau of Mineral Resources, Geology and Geophysics* 38: 65–96.

DICKINS, J. M., TOWNER, R. R. & CROWE, R. W. A., 1978. A Permian cold water marine fauna in the Grant Formation of the Canning Basin, Western Australia. *Journal of the Palaeontological Society of India* 20: 275–278.

ERLANGER, O. A., 1981. K revizii roda *Rhynchopora*. *Paleontologicheskii Zhurnal* 1981(1): 88–94.

FOSTER, C. B. & WATERHOUSE, J. B., 1988. The *Granulatisporites confluens* Oppel-zone and Early Permian marine faunas from the Grant Formation on the Barbwire Terrace, Canning Basin, Western Australia. *Australian Journal of Earth Sciences* 35: 135–157.

GLENISTER, B. F., ROGERS, F. S. & SKWARKO, S. K., 1993. Ammonoids. *Bulletin of the Geological Survey of Western Australia* 136: 54–63, 284–295 + microfiche supplement.

IVANOVA, E. A., 1972. Osnovnyye zakonomernosti evolyutsii spiriferid (Brachiopoda). *Paleontologicheskii Zhurnal*, 1972 (3): 28–42.

JONES, P. J. & YOUNG, G. C., 1993. Summary of Phanerozoic biostratigraphy and palaeontology of the Canning Basin (Lennard Shelf). *Record of the Australian Geological Survey Organisation* 1993/4: 1–62.

KING, W., 1865. Remarks on the histology of two specimens of *Rhynchopora geinitziana* de Verneuil, from near the River Oukhla, Province of Archangel. *Annals and Magazine of Natural History, Series 3*, 16: 124–128.

KÜHN, O., 1949. *Lehrbuch der Paläozoologie*. Stuttgart. 326 pp.

LIKHAREV, B. K., 1932. Notiz über Permische ablagerungen des Kolyma—Landes (Ost-Sibirien). *Izvestiya Akademii Nauk SSSR. Otdelenie Matematicheskikh i Estestvennykh Nauk, Seriya VII*, 1931(1): 93–98.

MERCER, C. R., 1967. Completion report BMR 8, Mount Madeline and 9, Daurie Creek, Byro Basin, Western Australia. *Report of the Bureau of Mineral Resources, Geology and Geophysics* 108: 1–19.

REDFERN, J., 1991. Subsurface facies analysis of Permo-Carboniferous glaciogenic sediments, Canning Basin, Western Australia. In *Gondwana Seven Proceedings*, H. Ulbrich & A. C. Rocha Campos, eds, Instituto de Geociencias da Universidade de Sao Paulo, Sao Paulo, 349–363.

PARFREY, S. M., 1986. Early Permian invertebrates from

the Camboon Andesite near Biloela, Southeastern Bowen Basin. *Geological Survey of Queensland, Publication* 387: 57–67.

REDFERN, J. & MILLWARD, E., 1994. A review of the sedimentology and stratigraphy of the Permo-Carboniferous Grant Group, Canning Basin, Western Australia. In *The Sedimentary Basins of Western Australia*, P. G. & R. R. Purcell, eds, Petroleum Exploration Society of Australia (WA Branch), Perth, 753–756.

SHI, G. R. & WATERHOUSE, J. B., 1991. Early Permian brachiopods from Perak, West Malaysia. *Journal of Southeast Asian Earth Sciences* 6: 25–39.

SOWERBY, J., 1820. *The Mineral Conchology of Great Britain; or Coloured figures and descriptions of those remains of testaceous animals or Shells, which have been preserved at various times and depths in the Earth.* W. Arding, London, vol. 3, 194 pp.

TOLMACHEV, 1. P., 1912. Materialy k' poznaniyu paleo-zoiskikh' otlozhenii Severo-Vostoehnoi Sibiri. *Trudy Geologicheskago Muzeya imeni Petra Velikago Imperatorskoi Akademii Nauk'* 6(5): 123–149.

TOLMATSCHOW (TOLMACHEV), 1. P., 1915. Materialen zur kenntnis der palaeozoischen Ablagerungen von Nord-Ost Siberien. *Zapiski Imperatorskago Mineralogicheskago Obshchestva, Vtoraya Seriya,* 50: 25–57.

WATERHOUSE, J. B., 1989. Middle and Late Carbon-iferous and Early Permian invertebrate faunas of Australia. *Onzieme Congres International de Stratigraphie et de Geologie du Carbonifere, Beijing 1987, Compte Rendu* 2: 361–375.

WHITFIELD, R. P., 1908. Notes and observations on Carboniferous fossils and semifossil shells, brought home by members of the Peary Expedition of 1905–1906. *American Museum of Natural History Bulletin* 24: 51–58.

AUSTRALIAN TERTIARY NEOLAMPADIDAE (ECHINOIDEA): A REVIEW AND DESCRIPTION OF TWO NEW SPECIES

Francis C. Holmes

15 Kenbry Road, Heathmont, Victoria 3135, Australia, *and* Department of Invertebrate Palaeontology,
Museum of Victoria, PO Box 666E, Melbourne, Victoria 3001, Australia

HOLMES, F. C., 1995:12:31. Australian Tertiary Neolampadidae (Echinoidea): a review and
description of two new species. *Proceedings of the Royal Society of Victoria* 107 (2):
113–128. ISSN 0035-9211.
    The age, stratigraphic horizon and distribution of each of the four known Australian
Tertiary neolampadids and their associated echinoid fauna is discussed in light of recent
discoveries. Two new taxa are described, the Late Eocene *Aphanopora*? *bassoris* sp. nov.
and the Early Miocene *Actapericulum bicarinatum* gen. et sp. nov. Variations in the posterior
profile and position of the periproct of *Pisolampas concinna* Philip 1963 and *Notolampas
flosculus* Philip 1963 are also discussed and analysed.
    With the discovery of *Aphanopora*? *bassoris* sp. nov., two distinct Cainozoic neolampadid
lineages are postulated; one with a monobasal apical system and the other a tetrabasal apical
system.

Keywords: Echinoidea, Neolampadidae, Tertiary, Australia, new taxa.

OF THE SEVEN monotypic genera previously assigned to the family Neolampadidae, only *Pisolampas* and *Notolampas* were known from the fossil record. Both of these have been found only in the Tertiary of southern Australia. The five extant genera have been reeorded from the China Sea (*Anochanus*); the South Sulu Sea and Norfolk Island (*Aphanopora*); western Timor (*Aphanopora* and *Nannolampas*); eastern Florida to the West Indies and Bahamas, eastern Atlantic coast from the Bay of Biscay to Morocco and the Mediterranean (*Neolampas*); and South Africa (*Tropholampas*) (Mortensen 1948; Mooi 1990). Baker & Rowe (1990) also refer to ?*Aphanopora* from New Zealand and the Kermadee Islands.

Since the description of *Pisolampas* and *Notolampas* (Philip 1963), extensive collecting in South Australia and Victoria by R. J. and F. Foster in the 1970s, and more recently by F. C. and E. Holmes, has uncovered two further Tertiary neolampadid species. One is tentatively assigned to *Aphanopora* de Meijere and the other to a new genus.

In addition, neolampadid specimens from Kangaroo Island and Yorke Peninsula, South Australia, show that *Notolampas flosculus* and, to a lesser extent, *Pisolampas concinna* have a noticeable degree of variation in the posterior profile and the position of the periproct, features not discernible in the material available at the time of their original description.

AGE, STRATIGRAPHY AND DISTRIBUTION

Late Eocene localities

Neolampadids are known from three Late Eocene loealities in southern Australia, each situated on the fringe of the St Vincent Basin, South Australia (Fig. I, locs 1–3).

The description of *Pisolampas concinna* Philip 1963 was based on speeimens from the Tortachilla Limestone, a Late Eocene (Aldingan, Bartonian-Priabonian) formation representing planktonic foraminiferal zones P14–15 (McGowran 1989). The Tortachilla Limestone, a yellow-brown, green and grey bioclastic limestone up to 2 m thick (Cooper 1979), crops out in the cliffs at the south end of Maslin Bay, about 40 km south of Adelaide (Fig. 1, loc. I). The formation contains a rich echinoid fauna including, in addition to *Pisolampas*, the cassiduloids *Apatopygus vincentinus* (Tate 1891), *Australanthus longianus* (Gregory 1890), *Echinolampas posterocrassa posterocrassa* Gregory 1890, and *Eurhodia australiae* (Duncan 1877), forms which possibly share a common ancestry with neolampadoids. Because of the southerly dip of the strata, the Tortachilla Limestone does not crop out south of Blanche Point at the southern end of the Bay (Reynolds 1953; Cooper 1979). Many echinoids collected in the nineteenth and early twentieth centuries, now clearly attributable to the Tortachilla Limestone,

were referred to as originating from Aldinga and Port Willunga to the south of Blanche Point where the predominate Late Eocene to Middle Miocene Port Willunga Formation is exposed in the coastal cliffs and shore platform.

About 90 km southwest of Maslin Bay, low coastal cliffs of yellow-buff bioclastic Kingscote limestone occur for about 2 km southwest of the Kingscote jetty, Kangaroo Island (Fig. 1, loc. 2). This limestone, variously regarded in the past century as of Miocene or Eocene age, was assigned a Late Eocene age in the 1950s based on correlation with the Tortachilla Limestone (Glaessner 1953). The formation has since been shown to comprise three distinct lithological units separated by disconformities. Only the lowest unit correlates in part with the Tortachilla Limestone, with which it shares a similar rich Late Eocene echinoid fauna. The middle and upper units range in age from Latest Eocene to early Late Oligocene (Milnes et al. 1983). In the northeastern exposure of the lowest unit, which crops out between the foreshore swimming pool and the jetty at Kingscote, the oldest of the two new neolampadids, *Aphanopora*? *bassoris* sp. nov., is known to occur with *Pisolampas concinna* and a small undescribed species of *Monostychia*? The most abundant echinoids, *Australanthus longianus, Echinolampas postero-*

crassa posterocrassa, and *Fibularia gregata* Tate 1885, occur mainly in the southwestern exposure of the unit just north of Brownlow Beach. Unfortunately, the exact locality and horizon within the Kingscote Limestone from which the majority of specimens have been collected in the past has not been recorded.

Approximately 95 km northwest of Maslin Bay exposures of the Muloowurtie Formation in the vicinity of Harts Mine (13 km south of Ardrossan) and at nearby Muloowurtie Point, eastern Yorke Peninsula (Fig. 1, loc. 3), constitute the third of the Late Eocene localities at which neolampadids have been identified. Based on faunal evidence, the Muloowurtie Formation (redefined by Stuart 1970) correlates with the lower unit of the Kingscote Limestone and in part with the Tortachilla Limestone (Milnes et al. 1983). However, apart from Tate (1891) recording *Apatopygus vincentinus*, and an extensive collection of over 100 small specimens of *Pisolampas concinna*, little seems to be known about the total echinoid fauna of the Muloowurtie Formation, Stuart (1970) recognising only *Fibularia gregata, Salenidia tertiaria* (Tate 1877) and *Eupatagus* sp.

Although three other major Late Eocene marine formations in southern Australia correlate in part with the Tortachilla Limestone, the lower beds of
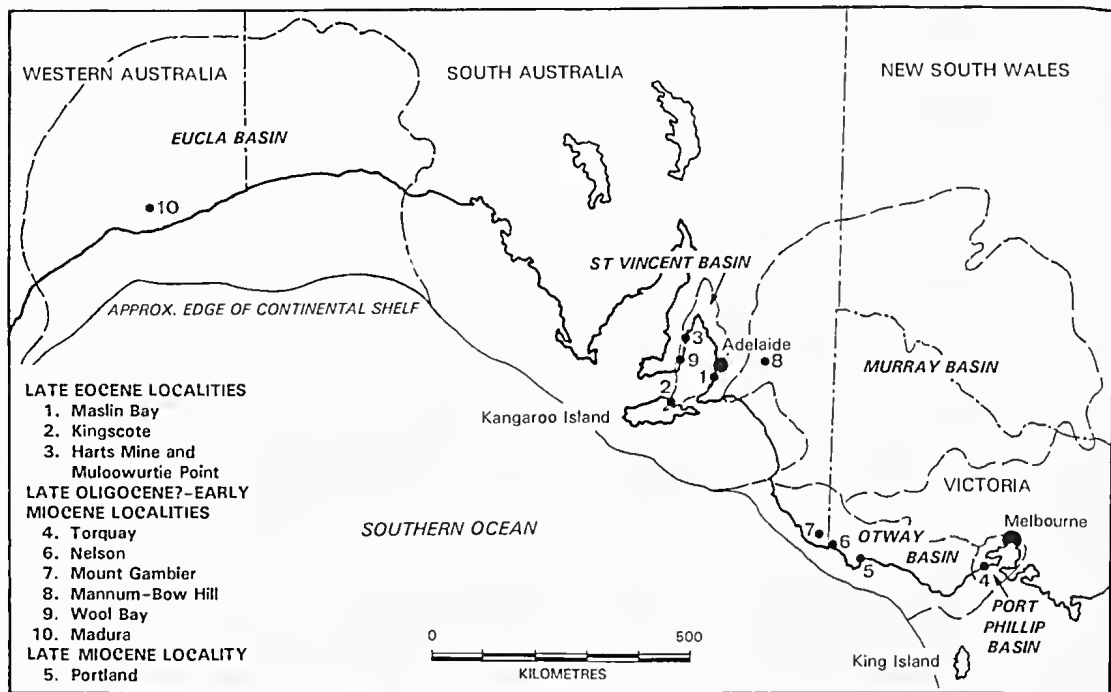
Fig. 1.   Distribution of Late Eocene–Late Miocene fossil neolampadids in southern Australia.

the Buccleuch Group (Beds A of Ludbrook 1961), South Australia, and the Wilson Bluff Limestone and Nanarup Limestone, Western Australia, so far no neolampadids have been recorded from these formations.

Latest Oligocene?–Early Miocene localities

In contrast to the apparently restricted distribution of the two Late Eocene species, what are generally considered to be Early Miocene neolampadids have so far been found in the Port Phillip Basin, Victoria (Fig. 1, loc. 4); the Otway Basin, South Australia and Victoria (Fig. 1, locs 6–7); the Murray Basin, South Australia (Fig. 1, loc. 8); the St Vincent Basin, South Australia (Fig. 1, loc. 9); and the Eucla Basin, Western Australia (Fig. 1, loc. 10).

The Zeally Limestone Member of the Puebla Formation, a yellowish sandy bryozoan calcarenite with thin calcirudite interbeds, is exposed in coastal cliffs in the vicinity of Torquay, about 80 km south of Melbourne (Fig. 1, loc. 4). Planktonic foraminifers present in the Zeally Limestone indicate a Longfordian to ?Batesfordian (Burdigalian–Langhian) age, corresponding approximately to zones N6–8 (Abele 1988).

Associated with *Actapericulum bicarinatum* gen. et sp. nov. in a narrow band at the base of the low cliff between 200 m and 300 m southwest of Point Danger, are the echinoids *Lovenia* sp. and *Orbispala occultoforma* Irwin 1995. A single specimen of *A. bicarinatum* has also been found associated with the marsupiate echinoid *Paraspatangus* sp. about 2–3 m above high tide level at Point Danger.

The Early Oligocene to early Middle Miocene Gambier Limestone has also yielded neolampadids in the vicinity of the South Australia–Victoria border. *Notolampas flosculus* is known from the predominantly soft, white, chalky limestone exposed in a working quarry south of Mt Gambier (Fig. 1, loc. 7); in cliffs near Princess Margaret Rose Caves on the banks of the Glenelg River; and in an old quarry about 1.6 km north of Nelson, Victoria (Fig. 1, loc. 6). So far, *Actapericulum bicarinatum* gen. et sp. nov. has only been recorded from the latter locality. Based on the age of the Gambier Limestone cropping out in the vicinity of Nelson (Abele, pers. comm. in Kenley 1971), an Early Miocene (Longfordian to ?Batesfordian) age (between zones N5 and N8) seems likely.

The Early Miocene (Longfordian, Aquitanian–Burdigalian) Mannum Formation, exposed primarily in cliffs along the Murray River between Swan Reach and Mannum, South Australia (Fig. 1, loc. 8), contains probably the richest echinoid fauna of any formation in Australia. However, as with Late Eocene material, little information exists on the exact location or stratigraphic horizon within the formation from which many early specimens were collected. In addition, the lack of published information on the stratigraphy of the Murray River cliffs makes it extremely difficult to determine the vertical distribution of any echinoid species. *Notolampas flosculus* Philip 1963 was described from specimens collected by Tate during the late nineteenth century from the general vicinity of Mannum. Ludbrook (1961) divided the type section of the Mannum Formation (Mannum pumping station) into lower and upper Members and listed the occurrence of various echinoids within each member; however, her identification of *Pygorhynchus vassali* Wright of Tate, 1891 (= *Notolampas flosculus*) in the lower of the two members is disputed by Philip (1963), who implies that Ludbrook's specimen is an *Echinolampas*. Although uncommon, specimens of *Notolampas flosculus* have been found over a fairly wide area; on the other hand, *Actapericulum* gen. nov. has so far been recorded from only one locality within the Mannum Formation, the cliffs adjacent to Coolcha Landing Recreational Reserve, 6.5 km west of Bow Hill. Specimens collected recently were found in a sparsely fossiliferous light yellow-brown bioclastic calcarenite about 20–23 m above mean river level near the top of the track leading down to the reserve. *Eupatagus rotundus* Duncan 1877, small *Fibularia gregata*, *Lovenia forbesii* (Tenison Woods 1862), *Ortholophus woodsi* (Laube 1869) and *Psephoaster klydonos* McNamara 1987, were found associated with the new genus.

In the St Vincent Basin, numerous specimens of *Notolampas flosculus* have been found in pale grey to dark yellowish grey bryozoan calcarenites and calcirudites of the Port Willunga Formation (= Port Vincent Formation in Stuart 1970) exposed in coastal cliffs between Stansbury and Edithburgh on the east side of Yorke Peninsula, South Australia (Fig. 1, loc. 9). As there is no stratigraphic break between the Oligocene and Miocene in the Port Willunga Formation no precise age can be given for the occurrence of *Notolampas*. However, based on the probable occurrence of the Oligocene–Miocene boundary in the cliffs (and adjacent quarry) at Klein Point, north of Wool Bay (Stuart 1970), and the gentle southerly dip of the strata to the south of Wool Bay, a latest Oligocene?–Early Miocene (Longfordian) age seems likely. Out of the 35 specimens of *Notolampas* from Yorke Peninsula, examined in the Museum of Victoria collections, 25 were found

between 0.75 and 2.25 km south of the jetty at Wool Bay where they are associated with *Echinolampas morgani* Cotteau 1890, a typical Early Miocene species.

At Madura (Fig. 1, loc. 10), in the Western Australian part of the Eucla Basin, specimens of *Notolampas* have been found in the yellowish porous bryozoan calcarenites and granule calcirudutes of the Early Miocene (Longfordian) Abrakurrie Limestone which disconformably overlies the Late Eocene Wilson Bluff Limestone (Hocking 1990). Philip (1970) identified *Pisolampas* sp. nov. in a field sample taken from just above the base of the Abrakurrie Limestone at Abrakurrie Cave (approx. 140 km east of Madura), and suggested that 'in the Abrakurrie Cave at least, the Wilson Bluff Limestone may pass conformably up into the Abrakurrie Limestone without any hiatus'. A search through Abrakurrie Limestone fossils held by the Geological Survey of Western Australia failed to locate this specimen, so the occurrence of *Pisolampas* in this formation cannot be confirmed.

Late Miocene locality

Recently, a single partially encrusted 20 mm long neolampadid almost certainly assignable to *Notolampas* has been found by Mr C. Ah Yee, associated with specimens of *Lovenia bagheerae* Irwin 1994 about 2 m above the base of the foreshore cliffs below the lighthouse at Portland, southwestern Victoria (Fig. 1, loc. 5). This section of the Port Campbell Limestone represents the upper part of zone N16 and the basal part of zone N17 (Singleton et al. 1976), making this specimen Mitchellian (Tortonian) in age and the youngest representative of *Notolampas*.

MATERIAL AND METHODS

The primary material on which this study is based is housed in the invertebrate palaeontological collection of the Museum of Victoria (specimen numbers prefixed NMV). Some secondary material used in statistical analysis is currently held in the author's private collection. Measurements were made with a dial calliper to an accuracy of 0.1 mm. Parameters are expressed as a percentage of test length (%TL) followed by the mean, the standard deviation (SD) and the number of specimens measured (N). In specimens of *Pisolampas concinna* and *Notolampas flosculus* variations in the height and width of the periproct are expressed as a percentage of test height (%TH) and test width (%TW) respectively.

SYSTEMATIC PALAEONTOLOGY

Order NEOLAMPADOIDA Philip, 1963

Suborder NEOLAMPADINA Philip, 1963

Family NEOLAMPADIDAE Lambert, 1918

Genus **Aphanopora** de Meijere, 1903

Type species. *Aphanopora echinobrissoides* de Meijere, 1903 (extant) from the Sawu Sea (Timor) and South Sulu Sea (Philippines); original designation.

Remarks. In his brief description of *Aphanopora echinobrissoides*, de Meijere (1903) did not separate generic and specific characteristics, although he later (de Meijere 1904) gave a clear generic diagnosis which is, with the possible exception of the reference to the periproctal plates, applicable to the fossil species described herein. Unfortunately de Meijere's diagnosis lacks any information on the apical plate structure, which presumably was not visible on either of his two specimens. Because of this lack of information on the type species, the Late Eocene species *A.? bassoris*, which is clearly tetrabasal, is only tentatively placed in *Aphanopora*.

Mortensen (1948), although noting that he had not seen these specimens, also included a generic diagnosis. This contains characteristics of the type species not used by de Meijere, namely: paired depressions in the adoral ambulacral plates; details of the primary spines and pedicellariae; and the lack of phyllodes or bourrelets. The latter reference contradicts de Meijere's statement that the floscelle is poorly developed. An abbreviated version of Mortensen's generic diagnosis is used by Durham & Wagner (1966). Two additional specimens of *Aphanopora echinobrissoides* from 240 km north of Norfolk Island were briefly described and figured by McKnight (1968), but no further information is added to de Meijere's (1904) description of the genus.

Aphanopora? bassoris sp. nov.

Figs 2A, B, 3A–M, 5I–L

Etymology. Latin *bassus*, meaning 'deep', and *oris*, meaning 'mouth', referring to the deeply sunken peristome. Noun in apposition.

Holotype. NMV P140922 from the Late Eocene (Aldingan, Bartonian?–Priabonian) Kingscote Limestone (lower bed), Kingscote, Kangaroo Island, South Australia; collected by L. McNeil, April 1990.

Paratypes. NMV P73675–P73682, P133072, P133073 and P140923 from the same member/horizon and locality as the holotype.

Other material. A single specimen in the private collection of Enid Holmes (EH 23), from the same member/horizon and locality as the holotype.

Diagnosis. Small moderately inflated ovoid neolampadids with centrally depressed adoral surface and greatest width and height posterior to centre. Apical system central, tetrabasal, with two gonopores. Ambulacra narrow, simple, non petaloid with a row of extremely small single pores in each half ambulacrum adorally. Phyllodes absent, bourrelets poorly developed. Peristome transversely oval, anterior of centre. Periproct supramarginal, longitudinally oval at the upper end of an elongated anal groove. Test evenly but not closely covered with small primary tubercles.

Description. Test small, specimens ranging from 9.7 to 11.0 mm in length (mean = 10.2 mm, SD = 0.4, N = 12), ovoid in outline at the ambitus with slight to moderately truncated posterior margin. Maximum width 87–93% TL (mean = 90.3%, SD = 2.1, N = 12) occurs 52–63% TL from anterior ambitus (mean = 57.6%, SD = 2.8, N = 12). Aboral surface moderately inflated, in lateral profile curving fairly steeply upwards from a well rounded anterior margin to reach a maximum height of 48–59% TL (mean = 53.3%, SD = 3.0, N = 12) between 50–64% TL from anterior ambitus (mean = 56.0%, SD = 4.2, N = 12) and, posterior of the apex, obliquely truncated to steeply curved. Viewed transversely, the aboral surface is evenly convex to obliquely truncated bilaterally and the adoral surface flat to mildly concave. The ambitus,

anteriorly and laterally, is situated at about 20% of the test height (TH) above the lowest point, rising to about 27% TH posteriorly. Both aboral and adoral surfaces of test have small randomly placed sunken primary tubercles generally uniform in size but slightly larger towards the ambitus.

Apical system basically central, ranging between 44–54% TL from anterior ambitus to centre line of gonopores (mean = 47.8%, SD = 3.1, N = 10), tetrabasal (ethmophract), anterior genital plates 2 and 3 being smaller than the adjoining posterior genital plates 1 and 4 which contain the two gonopores. Distinct dimorphism is present, female gonopores being markedly larger than those of male specimens of similar size. Ocular plates small; II, III, and IV in contact with apical disk, 1 and V separated from disk by first row of posterior interambulaeral plates. Up to 5 or 6 hydropores may be present anterior to the two gonopores in genital plate 2.

Ambulacra simple and relatively narrow, with the majority of plates containing a single primary tubercle. The presence of single pores in each column adapically cannot be determined although they occur adorally.

Interambulacra broad, each zone between three and four times width of adjoining ambulaeral zones at the ambitus, with individual plates very much larger adorally than adapically. Anterior interambulacra 2 and 3 narrower than others.

Floscelle not developed, although several specimens show signs of incipient bourrelets. While phyllodes do not appear to be present, in two
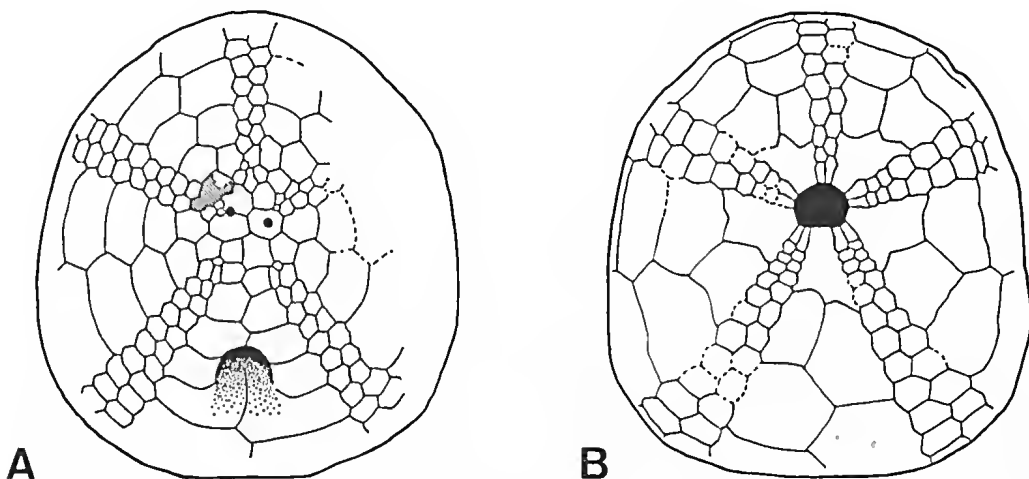
Fig. 2. *Aphanopora*? *bassoris* sp. nov.   A, adapical plating of paratype, NMV P140923 (♂).   B, adoral plating of paratype, NMV P133073 (♀).   Both ×5.5.
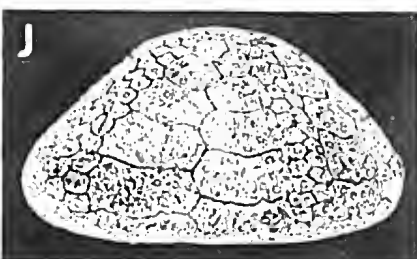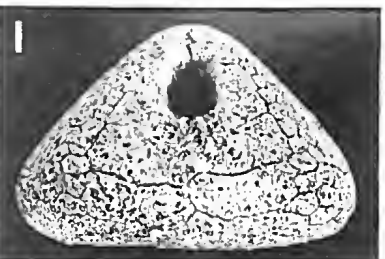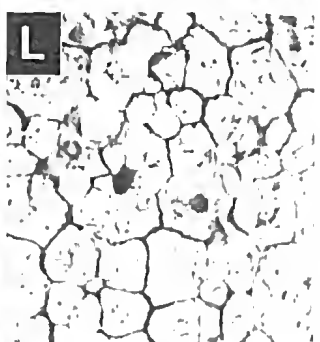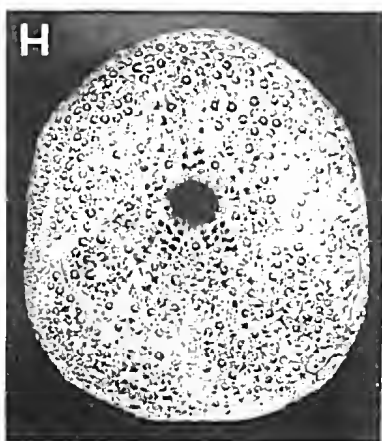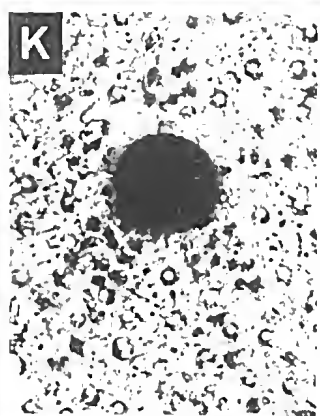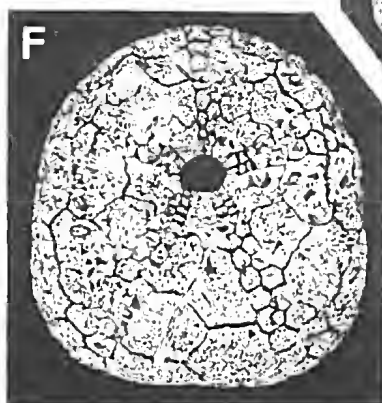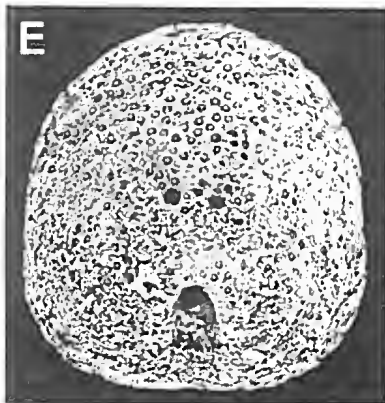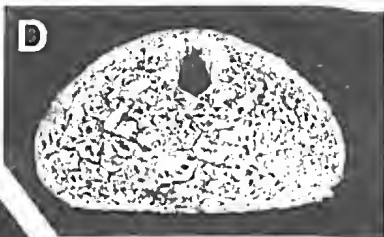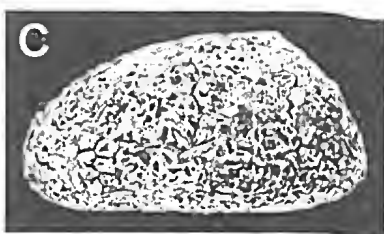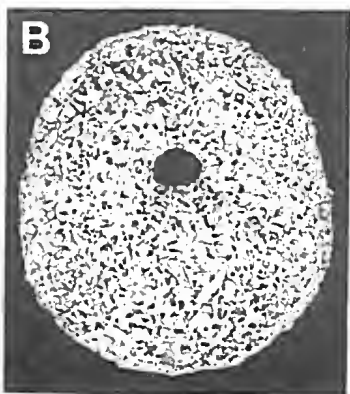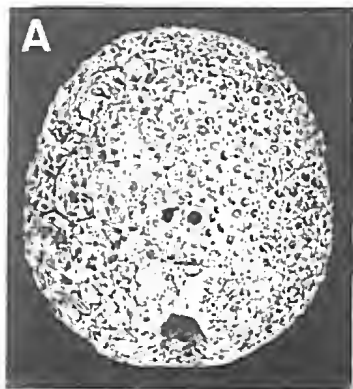
specimens there is evidence of pairs of very small, staggered, transversely elongated pits in ambulacral plates adjacent to the peristome (Fig. 3K, M). Buccal pores are also visible in one specimen.

Peristome anterior, transversely elliptical to sub-pentagonal, (width about 13% TL, length about 10.5% TL) at base of a deep well in shallow adoral depression situated 38–43% TL to centre from anterior ambitus (mean = 41.4%, SD = 1.3, N = 12).

Periproct supramarginal but not visible from above, small, subcircular to oval, deeper than wide, positioned nearly vertically beyond the anterior end of a moderately deep anal recess extending almost to the posterior margin. Anterior edge of anal groove 22–34% TL from posterior ambitus (mean = 28.7%, SD = 4.0, N = 12).

Remarks. De Meijere (1903, 1904) based his description of the extant type species partly on morphological features rarely, if ever, preserved in fossil specimens. While many of these features are well described and figured, details of the test shape are vague and can only be interpreted from very small sketches of the adoral surface and the lateral profile (de Meijere 1904: pl. 19, figs 372, 373) and one equally small photograph showing an oblique view of the adapical surface (pl. 6, fig. 79). In addition no information is given about the apical system plate structure, the location of the oculars or sexual dimorphism. A considerable number of features of *A.? bassoris*, appear to be almost identical to those of *A. echinobrissoides*, such as the ambulacral plating, tuberculation, shape and position of the peristome and periproct, and the occurrence of paired pits in the ambulacra adjacent to the peristome. However, when compared with de Meijere's illustrations and dimensions of *A. echinobrissoides*, *A.? bassoris* is very much smaller in size, proportionally higher and wider, lacks the apparent swelling below the ambitus in interambulacra 1 and 4 and lacks the concave 'pinched' lateral profile of the adapical and adoral surfaces posterior to the highest point.

McKnight's (1968) photographs of the adapical and adoral surfaces of one of the more recently collected specimens of *A. echinobrissoides* also show a considerable similarity with *A.? bassoris* in size and general appearance, although both the peristome and anal groove of the former appear to be very much wider. Unfortunately McKnight does not include either a posterior or lateral view of *A. echinobrissoides* and illustrations in Mooi (1990) appear to be only interpretations of McKnight's photographs.

Amongst other neolampadids, *A.? bassoris* appears to be most closely related to the extant species *Nannolampas tenera* (de Meijere 1903), both possessing tetrabasal apical systems with two gonopores. *N. tenera* is easily distinguished from *A.? bassoris* by its strongly truncated posterior and circular marginal periproct. The lack of a marsupium in female specimens distinguishes *A.? bassoris* from the poorly described *Anochanus sinensis* Grube 1868.

Genus **Pisolampas** Philip, 1963

Type species. *Pisolampas concinna* Philip, 1963 from the Late Eocene (Aldingan) Tortachilla Limestone of Maslin Bay, South Australia; original designation.

Diagnosis. See Philip (1963: 718).

Pisolampas concinna Philip, 1963

Figs 4, 5A–H

Pisolampas concinna Philip 1963: 719, pl. 106, figs 1–10, pl. 107, fig. 11, text-fig. 1a–c. — Durham & Wagner 1966: U630, fig. 516, 1a–d.

Remarks. Comparison of specimens of *Pisolampas concinna* from the Kingscote Limestone, Kangaroo Island (Fig. 1, loc. 2), and the Muloowurtie Formation, Yorke Peninsula (Fig. 1, loc. 3), with specimens from the type locality (Fig. 1, loc. 1), show that the species exhibits a noticeable variation in the height of the periproct above the base of the test (Fig. 5A–H). There are two fairly distinct groups; the periproct of specimens from the Kingscote Limestone being lower on the posterior face (marginal to slightly supramarginal) when compared with those from the Tortachilla Limestone and the Muloowurtie Formation, all of which are clearly supramarginal

---

Fig. 3. Aphanopora? bassoris sp. nov. All figures ×4.5 unless otherwise stated. A–D, holotype NMV P140922 (♀), adapical, adoral, lateral and posterior views. E, F, NMV P133073 (♀), adapical and adoral views. G–L, NMV P140923 (♂), adapical, adoral, posterior and lateral views; detail of peristomal area (×12); and detail of apical system (×12). M, NMV P73678 (♂), detail of paired pits and buccal pores in ambulacrum III adjacent peristome (×15). All specimens from the Late Eocene Kingscote Limestone, Kangaroo Island, South Australia.
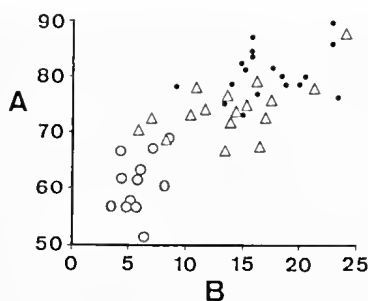
Fig. 4. Bivariate plot of periproct position in Late Eocene specimens of *Pisolampas concinna* Philip from the Kingscote Limestone (○), Muloowurtie Formation (●), and Tortachilla Limestone (△). A (vertical scale), height to top of periproct opening as % test height. B (horizontal scale), anterior end of anal recess to posterior ambitus as % test length.

(Fig. 4). While this variation is distinct in the specimens so far collected and examined, apart from a gradual increase in the length of the test of specimens from the Muloowurtie Formation (range 5.0–10.5 mm, mean = 6.87 mm, N = 35) through those from the Tortachilla Limestone (range 6.6–12.1 mm, mean = 9.61 mm, N = 22) to those from the Kingscote Limestone (range 9.8–15.4 mm, mean = 12.65 mm, N = 13), there are no other major differences. Even the test length to height, width, position of apex, widest point and peristome ratios remain virtually constant in specimens from the three formations. This evidence suggests that specimens from all three localities belong to a single, somewhat variable species rather than distinct subspecies.

Genus **Actapericulum** nov.

Etymology. Latin *acta*, meaning 'headland', and *periculum*, meaning 'danger', referring to the locality Point Danger, Victoria, from which the majority of specimens originate. Gender neuter.

Type and only known species. *Actapericulum bicarinatum* sp. nov.

Diagnosis. Small, mildly inflated, subcircular to ovoid neolampadids, with concave adoral surface and greatest width and height posterior to centre. Apical system monobasal, with four gonopores and small to moderately sized pierced oculars. Ambulacra with row of single pores in each column from phyllode to ocular. Elongated supramarginal periproct at anterior end of long deep anal groove extending to posterior margin. Peristome

longitudinally orientated, anterior of centre with well developed floscelle having clearly defined bourrelets and expanded phyllodes.

Remarks. The combination of four gonopores and an elongated supramarginal periproct easily distinguishes this genus from other neolampadids. *Tropholampas* H. L. Clark 1923, the only other neolampadid genus to have four gonopores, is very much smaller and has a highly inflated test, a marginal periproct and, in females, an adapical marsupium. Two other neolampadid genera are recorded as having elongated supramarginal periprocts, *Anochanus* Grube 1868 and *Aphanopora* de Meijere 1903; the former, although known only from a single specimen, can be distinguished from *Actapericulum* gen. nov. by the presence of an adapical marsupium; and the latter can be distinguished by the presence of only two gonopores, a transversely orientated peristome, rudimentary bourrelets and the lack of phyllodes.

The presence of a well developed floscelle in *Actapericulum* could be taken as evidence of a closer affinity with the cassiduloids rather than with other genera of neolampadids. However, the similarity between *Actapericulum* and the Late Eocene *Pisolampas*, the Early Miocene *Notolampas*, and the extant *Neolampas* in other characters (see Discussion on p. 126) necessitate placement in the Neolampadidae.

Actapericulum bicarinatum sp. nov.

Figures 6A–M, 8I–L

Etymology. Latin *bi*, meaning 'two', and *carinatus*, meaning 'keeled', referring to the pronounced adoral swelling of interambulacra 1 and 4.

Holotype. NMV P140924 from the late Early Miocene (Longfordian–?Batesfordian, Burdigalian–Langhian) Zeally Limestone Member, Puebla Formation, Point Danger, Torquay, Victoria; collected E. Holmes, September 1994.

Paratypes. NMV P73689–P73703, P73710–P73724, P140925, P140926 and P140929 from the same member/ horizon and locality as the holotype; NMV P73683 from the Early Miocene? of the Early Oligocene–early Middle Miocene Gambier Limestone, Mt Gambier, South Australia; NMV P73684–P73688 from the Early Miocene (Longfordian–?Batesfordian) Gambier Limestone, near Nelson, Victoria; and NMV P73704–P73709 from the Early Miocene (Longfordian) Mannum Formation, near Bow Hill, South Australia.

Other material. Two specimens (FCH1 and FCH2) from the Early Miocene (Longfordian) Mannum Formation, near Bow Hill, South Australia, in the author's private collection.

Diagnosis. As for genus.
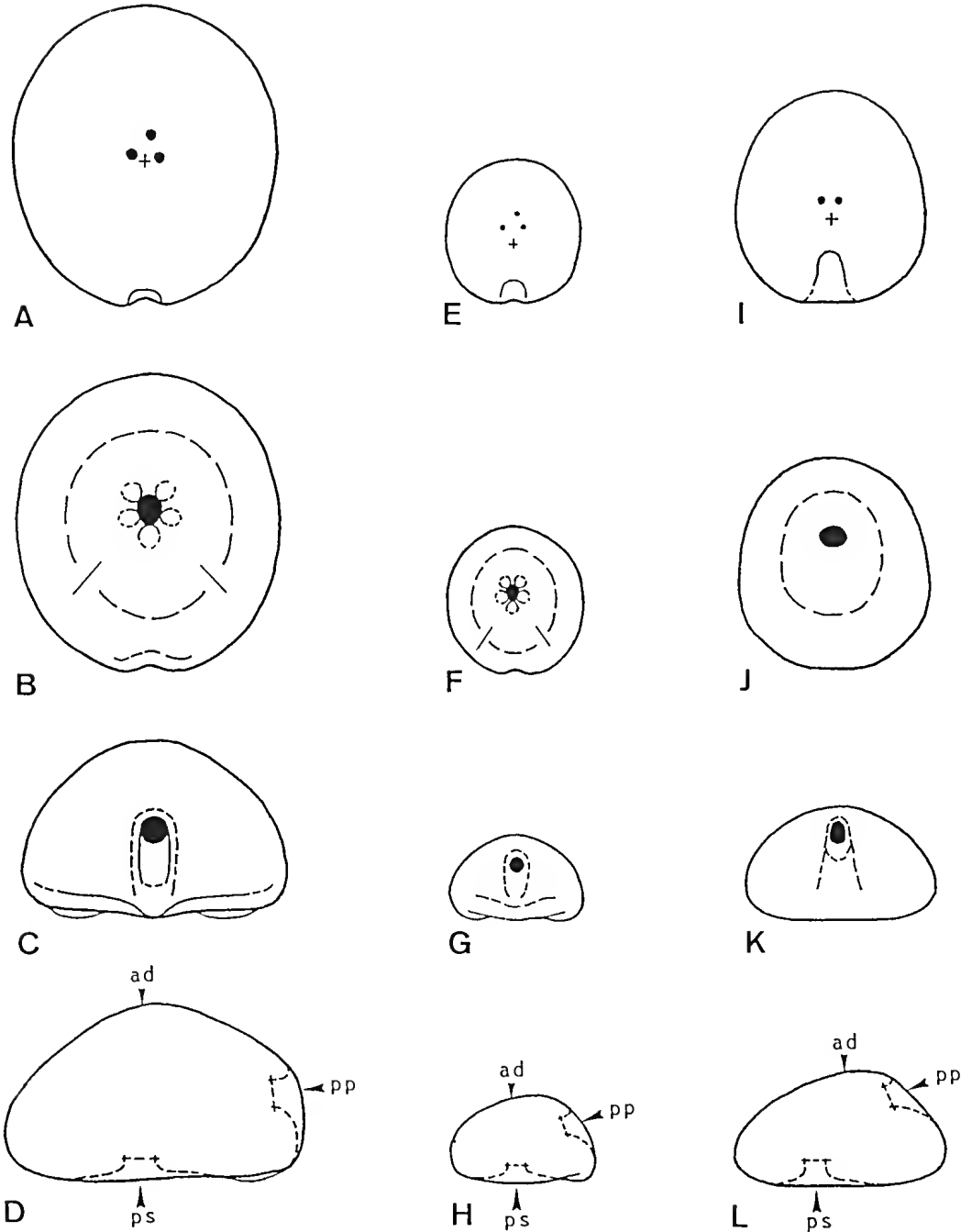
Fig. 5. Comparative drawings of Late Eocene neolampadids in adapical (A, E, I), adoral (B, F, J), posterior (C, G, K) and lateral (D, H, L) views; ×3. *Pisolampas concinna* Philip, A–C, NMV P140927 (♀) from the Kingscote Limestone, Kingscote, Kangaroo Island, South Australia; and E–H, NMV P73839 (?♀) from the Muloowurtie Formation, Muloowurtie Point, Yorke Peninsula, South Australia. *Aphanopora*? *bassoris* sp. nov., I–L, NMV P140922 (♀) from the Kingscote Limestone, Kingscote, Kangaroo Island, South Australia. Broken lines and arrows on lateral views indicate centre of apical disk (ad), periproctal recess (pp) and peristomal recess (ps).
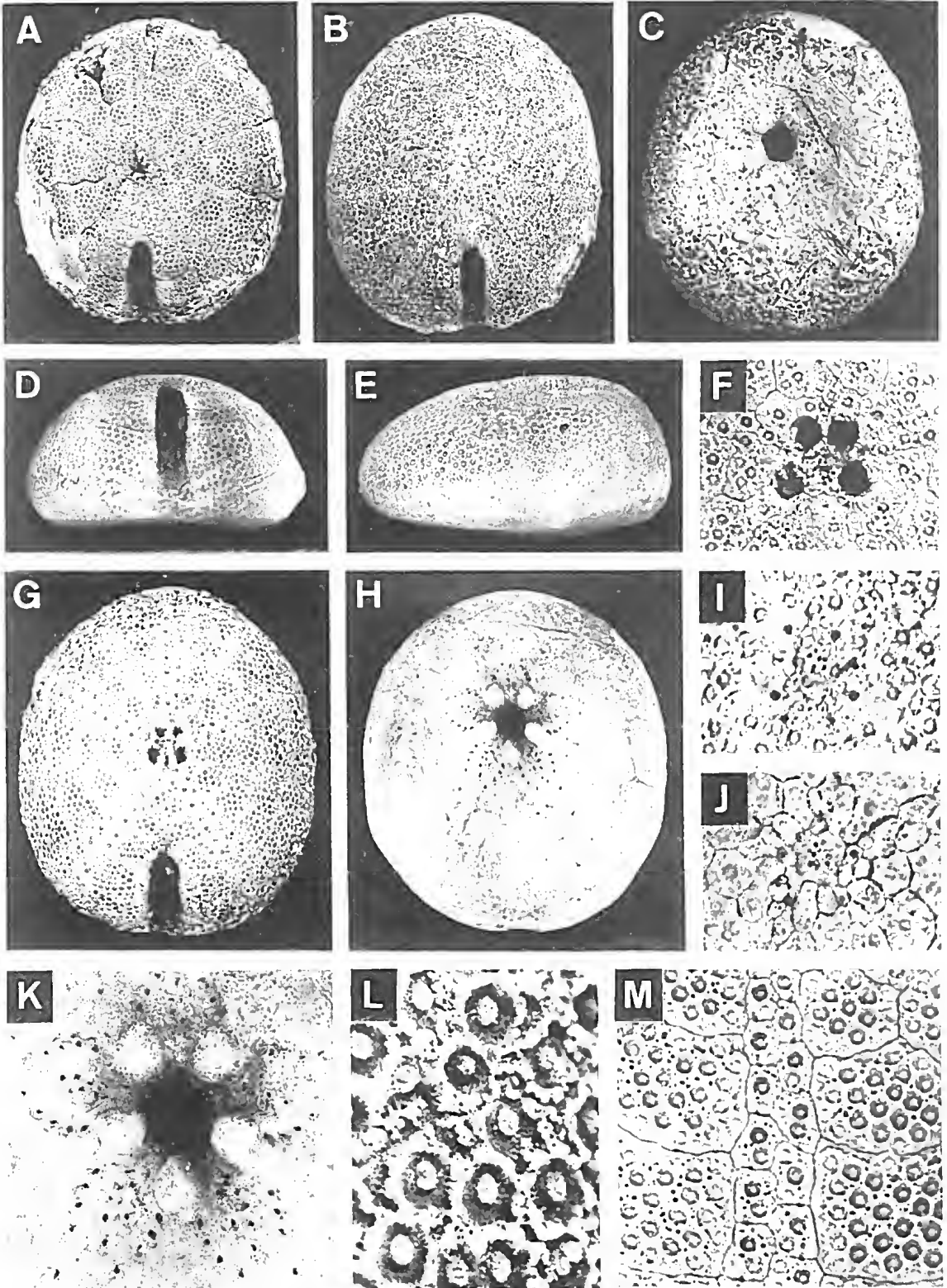
Description. Test small, specimens ranging from 9.6 to 16.4 mm in length (mean = 13.5 mm, SD = 1.9, N = 31), subcircular to ovoid in outline at the ambitus with slightly truncated posterior margin indented at base of anal groove. Maximum width 80–93% TL (mean 87.2%, SD = 2.7, N = 27) occurs 50–57% TL from anterior ambitus (mean = 53.4%, SD = 1.7, N = 27). Aboral surface mildly inflated, gently curving upwards from a well rounded anterior margin to reach a maximum height of 42–53% TL (mean = 48.6%, SD = 3.4, N = 17) between 51–59% TL from anterior ambitus (mean = 54.9%, SD = 2.8, N = 15). Posterior of the apex the aboral surface is more steeply curved, some specimens tending to be obliquely truncated in the vicinity of the anal groove. Transversely the aboral surface is evenly convex. Adoral surface flat or mildly depressed centrally with interambulacra 1 and 4 swollen below the ambitus to display a concave profile viewed anteriorly or posteriorly and a convex profile viewed laterally. The ambitus, anteriorly and laterally, is situated at about 30% of the test height (TH) above the lowest point (base of swollen interambulacra) rising to about 38% TH posteriorly. Both aboral and adoral surfaces of test covered with small closely spaced sunken crenulate and perforate primary tubercles (Fig. 6L).

Apical system slightly anterior of centre, 43–50% TL from anterior ambitus to centre (mean = 47.0%, SD = 2.1, N = 22), monobasal with four variably situated gonopores, anterior pair closer together than posterior pair. In the few male specimens where the plate structure can be observed, the four gonopores occur within the interambulacra on or close to the interradial sutures but generally in contact with the apical disk. However, in at least two specimens, two or more of the gonopores have migrated to the distal suture of one or other of the first pair of interambulacral plates and in another even into the second pair. Distinct dimorphism is present, female gonopores being very much larger than those of male specimens of similar size. Ocular plates variable in size, perforated by a single pore and generally in contact with the genital disk. Hydropores centrally located, usually between seven and ten in number but as many as fifteen may be present.

Ambulacra simple adapically, narrow, with row of small single pores in each column extending from phyllode to ocular, each pore situated adradially on, or immediately adjacent to the transverse suture between adjoining plates (Fig. 6M). Primary tubercles on ambulacral plates increase progressively in number from one in plates close to oculars to about six in plates at ambitus of large specimens.

Interambulacra broad, each zone between four and five times width of adjoining ambulacral zones at ambitus. Anterior interambulacra 2 and 3 slightly narrower than others, lateral interambulacra 1 and 4 swollen adorally.

Floscelle well developed with a gently rounded and moderately inflated granulated bourrelet in each interambulacrum, bulging slightly into the well of the peristome. Phyllodes variably expanded, but of even length, with large single pores in two series in each half ambulacrum, four or five pores in each outer series and usually one or two in each inner series although up to four may be present. The occurrence of occluded plates in the ambulacra can not be determined from available material. Buccal pores are present.

Peristome anterior, longitudinally subpentagonal to oval (length about 11% TL, width about 9% TL), moderately sunken and situated 39–43% TL to centre from anterior ambitus (mean = 41.1%, SD = 1.4, N = 20).

Periproct supramarginal and clearly visible from above, narrow, elongate, up to twice as long as wide, lying obliquely to the horizontal at the anterior end of a long deep anal groove extending to the posterior margin. Anterior end of anal groove 25–36% TL from outer edge of posterior indentation (mean = 28.9%, SD = 2.88, N = 27).

Remarks. Statistical analysis is based solely on the measurement of specimens from Point Danger, Torquay, Victoria (Fig. 1, loc. 4). Analyses of specimens from the Nelson-Mount Gambier area (Fig. 1, locs 6, 7) and from the Murray River near Bow Hill (Fig. 1, loc. 8) shows that both groups

---

Fig. 6. *Actapericulum bicarinatum* gen. et sp. nov.   All figures ×3.2 unless otherwise stated.   A, L, M, NMV P140925 (?♂), adapical view; detail of primary tubercles (×30); detail of adapical interambulacrum (×12). B, C, I, holotype NMV P140924 (♂), adapical and adoral views; detail of apical system (×12).   D, E, NMV P73685 (♂), posterior and lateral views; detail of apical system (×12).   F, NMV P140929 (♀), detail of apical system (×10).   G, NMV P73691 (♀), adapical view.   H, K, NMV P73689 (?), adoral view; detail of floscelle (×8).   J, NMV P140926 (♂) detail of apical system plate structure (×12).   NMV P73685 from the Early Miocene Gambier Limestone, Nelson, Victoria; all others from the Early Miocene Zeally Limestone Member, Puebla Formation, Torquay, Victoria.

fall well within the parameters set down for the new species. The only notable variations are the shorter anal groove in specimens from Nelson Mount Gambier; and the much smaller test size of those from near Bow Hill, the smallest being only 7.6 mm long.

Apart from the presence of an additional gonopore and the position of the periproct with its consequent effect on the posterior shape of the test, *A. bicarinatum* is similar to *Notolampas flosculus*, particularly in the detail of ambulacra, peristome and tuberculation. However, the floscelle in *A. bicarinatum* is more pronounced than in *N. flosculus*.

In the past, several authors have noted a strong superficial resemblance between some neolampadid genera and the cassiduloid *Apatopygus recens* (Edwards 1836). This resemblance is particularly noticeable in small specimens of *Actapericulum bicarinatum* from the Mannum Formation in South Australia, where a species of *Apatopygus* also occurs. However, the latter is easily distinguishable from *A. bicarinatum* by the presence of narrow open petals, pairs of pores, a transverse peristome, and the lack of a discernible floscelle.

Genus **Notolampas** Philip, 1963

Type species. Notolampas flosculus Philip, 1963 from the Early Miocene (Longfordian, Aquitanian-Burdigalian) Mannum Formation, near Mannum, South Australia; original designation.

Diagnosis. See Philip (1963: 719)

Notolampas flosculus Philip, 1963

Figs 7, 8A–H

Pygorhynchus Vassali Wright.—Tate 1891: 275
non *Pygorhynchus Vassali* Wright.—Duncan 1877: 41, 67.—Duncan 1887: 420.—H. L. Clark 1946: 358.—Ludbrook 1961: 44
Notolampas flosculus Philip 1963: 720, pl. 107, figs 1–10, text-fig. 2a, b.—Durham & Wagner 1966: U630, fig. 516, 2a–d.—Sadler, Pledge & Morris 1983: 27.

Remarks. Examination and measurement of 47 specimens of *Notolampas flosculus*, in the Museum of Victoria collections, indicate a great deal of variation in the position of the periproct, variation not evident in the seven specimens on which the original description was based. These more recently collected specimens, ranging in length from 8.0 mm to 19.0 mm, are from the Gambier Limestone near Mount Gambier, South Australia and near Nelson, Victoria; the Mannum Formation near Mannum, South Australia; and the Port Willunga

Formation near Stansbury, Yorke Peninsula, South Australia (Fig. 1, locs 6–9). The variation shows a continuous gradation between very distinct end members and is not related to the different collection localities. At one end of the range is a specimen similar to the type material but with interambulacrum 5 markedly swollen on the adoral surface anterior to the submarginal periproct (Fig. 8A–D), whereas at the other end there are two specimens in which the periproct is supra-marginal, being very high on the semitruncated posterior surface above the ambitus but still obscured from above by a projecting lip in interambulacrum 5 (Fig. 8E–H). Intermediate forms have the periproct at varying heights above the lowest point of the test and the angle of the posterior laterally truncated adoral surface ranging between 40° and 85° to the horizontal. In all cases the recessed opening of the periproct is not visible from above, and, except in two or three specimens, it is not visible from the posterior. The overall variability of these features (Fig. 7) precludes recognition of two distinct subspecies.

The only significant differences between the specimens from the three localities are: the greater test height of specimens from the Port Willunga Formation (mean = 53.7% TL) and Mannum Formation (mean = 52.5% TL) compared to those from the Gambier Limestone (mean = 44.1% TL); and the much narrower width of the periproct in specimens from the Mannum Formation (mean = 12.6% TW) than in those from the Port Willunga
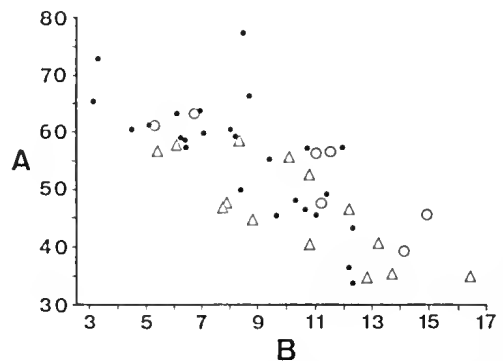
Fig. 7. Bivariate plot of periproct position in Early Miocene specimens of *Notolampas flosculus* Philip from the Gambier Limestone (○), Mannum Formation (△) and Port Willunga Formation (●). A (vertical scale), height to underside of lip or beak overhanging periproct as % test height. B (horizontal scale), anterior end of anal recess to posterior ambitus as % test length.
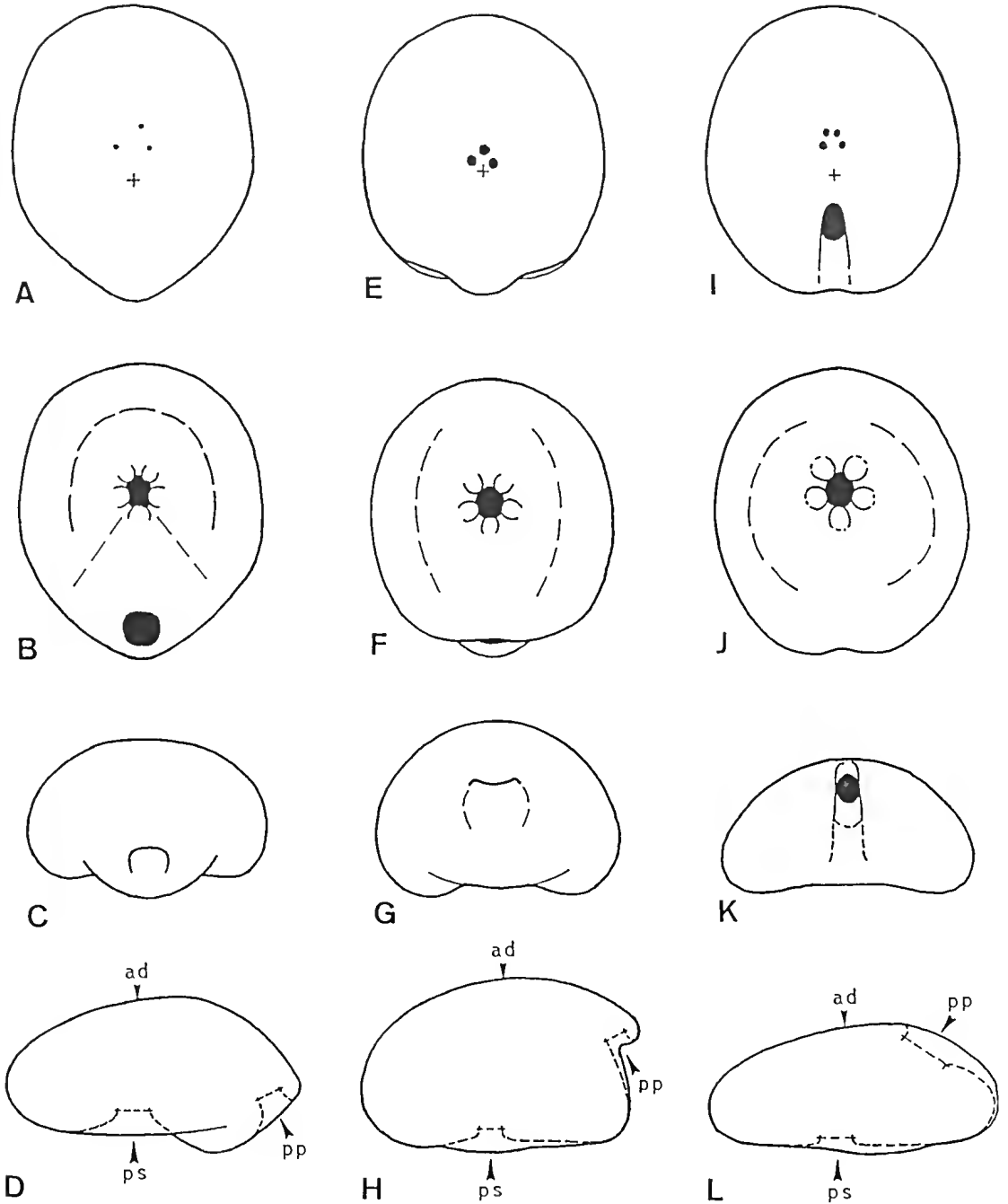
Fig. 8. Comparative drawings of Late Oligocene?–Early Miocene neolampadids in adapical (A, E, I), adoral (B, F, J), posterior (C, G, K) and lateral (D, H, L) views, ×3. *Notolampas flosculus* Philip, A–D, NMV P140928 (♂) from the Mannum Formation, Younghusband, South Australia; and E–H, NMV P145090 (♀) from the Port Willunga Formation, Stansbury, Yorke Peninsula, South Australia. *Actapericulum bicarinatum* gen. et sp. nov., I–L, NMV P73701 (♀) from the Zeally Limestone Member, Puebla Formation, Point Danger, Torquay, Victoria. Broken lines and arrows on lateral views indicate centre of apical disk (ad), periproctal recess (pp) and peristomal recess (ps).

Formation (mean = 17.0% TW) and the Gambier Limestone (mean = 17.8% TW). These features by themselves are also not considered sufficient to justify the recognition of subspecies.

DISCUSSION

The discovery of the non-marsupiate Late Eocene *Aphanopora*? *bassoris* almost certainly refutes the suggestion (Mortensen 1948; Durham and Wagner 1966; McKnight 1968; Mooi 1990) that the two specimens on which the extant genus *Aphanopora* is based are males of the extant genus *Anochanus*, the only known specimen of which is marsupiate.

This Late Eocene discovery also clearly shows that at least two distinct neolampadid lineages have existed for most, if not the whole of the Cainozoic Era. One lineage, with a monobasal apical system, moderately well developed floscelle, and ambulacral pores extending from the peristome to the apical system, is represented by the Late Eocene *Pisolampas*, the Early Miocene *Actapericulum* and *Notolampas*, and the extant *Neolampas* (A. Agassiz 1869). The other lineage, with a tetrabasal apical system, no discernible floscelle, and aboral ambulacral pores atrophied or possibly absent, is represented by the Late Eocene *Aphanopora*? *bassoris*, the extant *Nannolampas* (based on Mortensen's 1948 description and illustration), and probably the extant *Aphanopora echinobrissoides* (the apical system plate structure of this latter species is undescribed).

The two extant marsupiate genera *Anochanus* and *Tropholampas* cannot easily be placed in either of the above lineages, the former because of the lack of any detailed description or illustration (although Grube [1868] stated that the rows of single ambulacral pores extend from the peristome to the apical system), and the latter because of its monobasal apical system but lack of any discernible floscelle. However, *Tropholampas* is similar in one respect to some, but not all, specimens of *Pisolampas concinna* in having the ambulacral columns and oculars separated from the monobasal genital plate by the interambulacra.

Stefanini (1913), Mortensen (1948), Philip (1963), and Durham & Wagner (1966) have each in turn postulated a cassiduloid ancestry for the neolampadids. Durham & Wagner (1966), in raising the group to ordinal status, stated that the lack of petals adapically and the nature of the ambulacral pores suggest that the neolampadids are secondarily specialised from a cassiduloid ancestry or were derived from an ancestor with poorly developed bourrelets and petals. In a study based only on extant genera, Mooi (1990) recognised only the familial standing of the neolampadids, placing them in the Cassiduloida pending phylogenetic revision of the order's living taxa.

The discovery of the two additional fossil species, and the obvious separation of genera into at least two lineages, strongly reinforces the view of Mortensen (1948) that the Neolampadidae may not be a natural family. Further, Suter (1994) in a cladistic analysis of living cassiduloids, including neolampadids and three representative clypeasteroids, noted that phylogenies based on 'taphonomically robust' characters likely to be preserved in fossils, fail to support neolampadid monophyly. Suter also noted that, in all analyses carried out, the neolampadids form the sister group of the clypeasteroids, with most of the analyses placing the cassidulid genus *Studeria* (a species of which occurs in the Early Miocene of Australia) as the sister taxon to the neolampadid clypeasteroid clade.

ACKNOWLEDGEMENTS

REFERENCES

ABELE, C., 1988. Central coastal basins. In *Geology of Victoria*, 2nd edn, J. G. Douglas & J. A. Ferguson eds, Victorian Division, Geological Society of Australia Incorporated, Melbourne, 303–322.

AGASSIZ, A., 1869. Preliminary report on the Echini and starfishes dredged in deep water between Cuba and the Florida Reef, by L. F. de Pourtales. *Bulletin of the Museum of Comparative Zoology* 1: 253–308.

BAKER, A. N. & ROWE, F. W. C., 1990. Atelostomatid sea urchins from Australian and New Zealand waters (Echinoidea: Cassiduloida, Holasteroida, Spatangoida, Neolampadoida). *Invertebrate Taxonomy* 4: 281–316.

CLARK, H. L., 1923. The echinoderm fauna of South Africa. *Annals of the South African Museum* 13: 221–435, pls 8–23.

CLARK, H. L., 1946. The echinoderm fauna of Australia, its composition and its origin. *Carnegie Institute of Washington, Publication* 566: 1–567

COOPER, B. J., 1979. Eocene to Miocene stratigraphy of the Willunga Embayment. *Department of Mines and Energy, Geological Survey of South Australia Report of Investigations* 50: 1–101.

COTTEAU, G., 1890. Échinides nouveaux ou peu connus (9th article). *Mémoires de la Société Zoologique de France* 3: 537–550, pls 11, 12.

DUNCAN, P. M., 1877. On the Echinodermata of the Australian Cainozoic (Tertiary) deposits. *Quarterly Journal of the Geological Society of London* 33: 42–73.

DUNCAN, P. M., 1887. A revision of the Echinoidea from the Australian Tertiaries. *Quarterly Journal of the Geological Society of London* 43: 411–430.

DURHAM, J. W. & WAGNER, C. D., 1966. Neolampadoids. In *Treatise on Invertebrate Paleontology, Part U, Echinodermata* 3 (2 vols), R. C. Moore, ed., The Geological Society of America Inc. & The University of Kansas Press, U628–630.

EDWARDS, H. Milne, 1836. *Les Zoophytes ou animaux rayonnés. (Le Règne Animal distribue d'après son Orginasation, pour servir de base a l'histoire naturelle des animaux, et d'introduction a l'anatomie comparé*, by George Cuvier, 3rd edn), Fortin, Masson et Cie, Libraries, Paris, 190 p, 97 pls.

GLAESSNER, M. F., 1953. Conditions for Tertiary sedimentation in southern Australia. *Transactions of the Royal Society of South Australia* 76: 141–146.

GREGORY, J. W., 1890. Some additions to the Australian Tertiary Echinoidea. *The Geological Magazine* 27: 481–492, pls 13, 14.

GRUBE, E., 1868. Über einen lebendig gebärenden Seeigel. *Monatsberichte der königlich preussischen Akademie der Wissenschaften zu Berlin* aus dem Jahre 1868: 178–180. [English language translation in *Annals and Magazine of Natural History* (4)2: 168–170.]

HOCKING, R. M., 1990. Eucla Basin. *Geological Survey of Western Australia Memoir* 3: 548–561.

IRWIN, R. P., 1994. The spatangoid echinoid *Lovenia* from the Tertiary of southeastern Australia. *Proceedings of the Royal Society of Victoria* 106: 1–15.

IRWIN, R. P., 1995. New family and genus of Clypeasteroida (Echinoidea) from the Australian Tertiary. *Memoirs of the Association of Australasian Palaeontologists* 18: 189–198.

KENLEY, P. R., 1971. Cainozoic geography of the eastern part of the Gambier Embayment, southwestern Victoria. In *The Otway Basin of southeastern Australia* (Special Bulletin of the Geological Surveys of South Australia and Victoria), H. Wopfner & J. G. Douglas, eds, Government Printer, Adelaide, 89–153.

LAMBERT, J., 1918. Considérations sur la classification des Echinides Atélostomes. 1. Brachygnata (sic) et Procassiduloida. *Mémoire Société Academique, d'agriculture, des sciences, arts et belles lettres du department de l'Aube* 82: 1–48.

LAUBE, G. C., 1869. Über einige fossile Echiniden von den Murray Cliffs in Sud-Australien. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften zu Wein* 59: 183–198.

LUDBROOK, N. H., 1961. Stratigraphy of the Murray Basin in South Australia. *Geological Survey of South Australia Bulletin* 38: 1–96, pls 1–8.

McGOWRAN, G., 1989. The later Eocene transgressions in southern Australia. *Alcheringa* 13: 45–68.

McKNIGHT, D. G., 1968. Some echinoids and ophiuroids from off Norfolk Island and from Wangenella Bank. *New Zealand Journal of Marine and Freshwater Research* 2: 204–213.

McNAMARA, K. J., 1987. Taxonomy, evolution, and functional morphology of southern Australian Tertiary hemiasterid echinoids. *Palaeontology* 30: 319–352.

MEIJERE, J. C. H. de, 1903. Vorläufige Beschreibung der neuen, durch die Siboga-Expedition gesammelten Echiniden. *Tijdschrift der Nederlandsche Dierkundige Vereeniging*, ser. 2, 8: 1–16.

MEIJERE, J. C. H. de, 1904. Die Echinoidea der Siboga-Expedition. *Siboga-Expeditie (Uitkomsten op Zoologisch, Botanisch, Oceanographisch en Geologisch Gebied verzameld in de Oost-Indische Archipel 1899–1900 aan board H.M. Siboga. . .)*, monograph 43 [also published as vol. 29, *Echinodermata B*], M. Weber & L. F. de Beaufort, eds, E. J. Brill, Leiden, 252 p, 23 pls.

MILNES, A. R., LUDBROOK, N. H., LINDSAY, J. M. & COOPER, B. J., 1983. The succession of Cainozoic marine sediments on Kangaroo Island, South Australia. *Transactions of the Royal Society of South Australia* 107: 1–15.

MOOI, R., 1990. Living cassiduloids (Echinodermata: Echinoidea): a key and annotated list. *Proceedings of the Biological Society of Washington* 103: 63–85.

MORTENSEN, T., 1948. *A monograph of the Echinoidea 4(1). Holectypoida, Cassiduloida*. C. A. Rietzel, Copenhagen, 371 p, 14 pls.

PHILIP, G. M., 1963. Two Australian Tertiary neolampadids, and the classification of cassiduloid echinoids. *Palaeontology* 6: 718–726.

PHILIP, G. M., 1970. Appendix 1—Tertiary echinoids from the Eucla Basin. *In* Geology of the Western Australian part of the Eucla Basin. *Bulletin of the Geological Survey of Western Australia* 122: 182–191, pl. 5.

REYNOLDS, M. A., 1953. The Cainozoic succession of Maslin and Aldinga Bays, South Australia. *Transaction of the Royal Society of South Australia* 76: 114–140.

SADLER, T., PLEDGE, N. S. & MORRIS, B., 1983. *Fossils of South Australia. Part 1: Sea urchins of the Murray River cliffs*. Quoll Enterprises, Seaton, South Australia, xxx + 34 p.

SINGLETON, O. P., McDOUGALL, I. & MALLETT, C. W., 1976. The Pliocene–Pleistocene boundary in southeastern Australia. *Journal of the Geological Society of Australia* 23: 299–311.

STEFANINI, G., 1913. Probabile origine neotenica degli ambulacri di *Neolampas. Atti dell'Accademia scientifica veneto-trentino-istriana* 3(6): 33–41.

STUART, W. J. Jnr, 1970. The Cainozoic stratigraphy of the eastern coastal area of Yorke Peninsula, South Australia. *Transactions of the Royal Society of South Australia* 94: 151–178.

STUDER, T., 1881. Übersicht über die während der Reise S. M. S. Corvette Gazelle um die Erde 1874–76 gesammelten Echinoiden. *Monatsberichte der königlich preussischen Akademie der Wissenschaften zu Berlin* aus dem Jahre 1880: 861–879.

SUTER, S. J., 1994. Cladistic analysis of the living cassiduloids (Echinoidea), and the effects of character ordering and successive approximations weighting. *Zoological Journal of the Linnean Society* 112: 363–387.

TATE, R., 1877. On a new species of *Belemnites* and *Salenia* from the Middle Tertiary of South Australia. *Quarterly Journal of the Geological Society of London* 33: 256–259.

TATE, R., 1885. Miscellaneous contributions to the Palaeontology of the older rocks of Australia. *Southern Science Record* 1 (n.s.): 1–5.

TATE, R., 1891. A bibliography and revised list of the described echinoids of the Australian Eocene, with descriptions of some new species. *Transactions and Proceedings and Report of the Royal Society of South Australia* 14: 270–282.

TRUSWELL, E. M., CHAPRONIERE, G. C. H. & SHAFIK, S. (compilers), 1991. Australian Phanerozoic Timescales: 10, Cainozoic Biostratigrapic Chart and Explanatory Notes. *Bureau of Mineral Resources, Australia, Record* 1989/40: iv + 16 p. and chart.

WOODS, J. E. Tenison, 1862. *Geological observations in South Australia, principally in the district southeast of Adelaide.* Longman Green, Longman, Roberts and Green, London, xviii + 404 p.

TRANSACTIONS

ROYAL SOCIETY OF VICTORIA

J. E. CUMMINS OBE, MEMORIAL ORATION

PREFACE

Ours is a scientific Society; and to twist an ancient quote: 'scientists, of all people, understand business the least'.

On 25 May 1995 your Society held a most successful symposium on science policy; and it has been recorded in this volume as Transactions. This was scientists talking to scientists.

To these Transactions has been added the Cummins Oration given by John Prescott on 22 August. The decision of your Council to include the Oration was made because of the obvious and urgent need for scientists to better understand business and businessmen. Science can no longer afford to remain separate from the mainstream activities of the community and the economy.

As governments contract their own spending, and as they vacate ever-broadening areas of the economy to business, expectations for further change build up. The trend is world-wide—applying in Beijing as well as Melbourne; and it is still accelerating. It can hardly be reversed in our lifetimes.

We all know that business doesn't yet understand science sufficiently well, but that is no reason why science should fail to understand business.

John Prescott is Australia's premier businessman. As Managing Director of BHP, he leads a company over 100 years old which, by most measures in most years, is Australia's largest.

BHP is a company which exports to the world, competes against imports in our domestic market, and invests, constructs and operates on a vast scale in Australia and overseas. It is a company with a large and far-flung workforce which must be motivated and coordinated. Lastly, it is a company which must and does work with our government at the national level; neither can ignore the other.

These attributes qualify John Prescott to speak on the future of Australia, and on the roles in it of business and government. What he has written here is worth reading.

J. E. CUMMINS

The inaugural Oration of the Sciences Club took place in 1974, the Orator being Sir Louis Matheson. Thus a tradition was begun which has continued each year without interruption until the present time.

In 1989, following the death of J. E. Cummins OBE, the title of the Oration was changed to the J. E. Cummins OBE Memorial Oration to honour the man who was principally responsible for the erection of the National Science Centre which was completed in 1967.

In the early 1960s the idea was conceived within the CSIRO in which J. E. Cummins was a senior scientist, of a building which would house Scientific, Technological and Learned Societies at a reasonable rental. It was envisaged that the Centre would provide the opportunity for the interchange of ideas and a furtherance of knowledge.

J. E. Cummins (Jack as he was known), was personally responsible for raising most of the funds to build the National Science Centre, known also as Clunies Ross House. He approached many individuals and large and small corporations both here and overseas and his success can be judged from the fact that, when completed, the building was free of debt.

It was Jack who conceived the idea that Clunies Ross House should contain a venue where members of various Scientific and Technological Societies could meet in an informal manner. Thus it was that The Sciences Club became the social centre of Clunies Ross House.

Jack became the inaugural President of The Sciences Club in 1968. He was appointed to the Board of Governors of Clunies Ross House in 1971, retiring in the year of his death.

A change in the philosophy of the Board of Governors in the late 1980s resulted in The Sciences Club vacating Clunies Ross House in July 1990 and merging with the Royal Society of Victoria on 1 January 1991.

It is sad to reflect on the disintegration and demise of such a wonderful and idealistic concept. The Scientific, Technological and Learned Societies are once more scattered throughout Melbourne and the National Science Centre at 191 Royal Parade, Parkville has been partly demolished and redesigned as an apartment block.

MARGARET C. HARRIS
President of The Sciences Club 1990–1991

23

PARTNERS IN GROWTH: THE ROLE OF BUSINESS AND GOVERNMENT IN PROMOTING PROSPERITY

by JOHN B. PRESCOTT

Managing Director and Chief Executive Officer, The Broken Hill Proprietary Company Limited

Held at the Royal Society's Hall, 9 Victoria Street, Melbourne, on 22 August 1995

INTRODUCTION

I am honoured to have been asked to give the J. E. Cummins Memorial Oration. I hope that my remarks this evening on how government and business can promote our national prosperity will be as provocative as past orations by Sir Ian McLennan, Sir Arvi Parbo and Professor Adrienne Clarke and other distinguished speakers.

My theme tonight is 'Partners in Growth — the role of business and government in promoting prosperity'.

Before detailing what I see as the key elements of such a partnership, let me set the context.

SETTING THE SCENE

We live in a world where the dynamics of economics and technology have largely escaped the constraints of national territory. It is a world where the passport to success is stamped with confidence, excellence and single-minded purpose.

Just a few months ago, the Australian cricket team showed great purpose and self-belief in beating the West Indies — a side that had gone for more than 20 years without defeat in a series at home.

Across the world, many Australians excel in the arts, in science, in films, in sport and in business. Outstanding as the achievements of these individuals and groups of individuals are, we need to go further.

- As a nation we need to become as purposeful and as confident as our world class compatriots in meeting the main challenge of our era — the intellectual, economic and technological competition between nations.
- In that contest, a nation can go from being a champion to an 'also ran' within a generation. Conversely, they can transform themselves just as swiftly from an 'also ran' into a champion.
- A nation's standing is largely determined by how it responds to the demands of change — and there are many examples of both upward and downward movement.

GLOBAL LESSONS

People who grew up in the 1950s will recall the boast by the then leader of the Soviet Union, Nikita Khrushchev, 'we will bury you'. Despite the military tensions of those days, Khrushchev had in mind an economic and scientific triumph over the Western world. The Soviet economy was growing very strongly at that time, and their space program was then the pace setter.

Within a generation however, that seemingly formidable challenge evaporated. The command economy and the political system that underpinned it was completely unable to embrace change — it was not able to allow for the creativity and aspirations or even the basic needs of people, which is absolutely integral to the advancement of a nation.

Closer to home and in our time, a nation that has been Australia's economic partner for more than a generation is now undergoing a subtle yet profound national transformation.

Like many others who have visited Japan frequently over the years, my visits have confirmed my admiration for Japan's achievements. Even amidst that country's current difficulties, the performance of the Japanese economy and the exploits of their outstanding companies over past decades have caused economists to re-write the textbooks. However, despite past achievements, today there are powerful pressures for change both from within Japan and from countries such as the United States.

Thoughtful voices for change are to be found within Japan itself. With considerable justification, they claim that despite their country's status as an economic superpower, Japanese consumers, have not gained the full benefit of the country's standing. Prices of goods and services are higher — albeit declining — than would be the case if there was a concerted liberalisation of Japan's domestic economy.

Even in that nation, it is clear that nothing can be constant.

RELEVANCE FOR AUSTRALIA

- I think the experience of Japan holds powerful lessons for Australia.

We cannot fall into the trap of thinking that the reforms we have instituted so far are enough to secure our future. A country must be able to constantly renew itself if it is to offer its people rising standards of living and larger opportunities.

The experiences of Japan and other seemingly strong economic powerhouses confirm the need for a policy framework that can deal with contemporary challenges, rather than being satisfied with past achievements.

- I believe that we need to take initiatives in three areas to help create a framework for national prosperity:

    we need to get the broad economic settings right for sustainable growth;

    we must revitalise our economic and intellectual infrastructure; and

    firms and governments and society as a whole must instil in their people a new sense of initiative.

I think these three elements are key building blocks for prosperity in the contemporary world.

First, some comments on the role of governments.

ROLE OF GOVERNMENT IN THE GLOBAL ECONOMY

In the 'borderless world' of rapid flows of technology, goods and services and investment, there are economic forces that are increasingly beyond the control of governments. Those that intervene to artificially distort trade and investment flows are not likely to succeed. But there is an important role for governments in positively influencing the international trade environment, and in encouraging domestically an efficient and socially responsible business sector that is able to compete strongly in the global marketplace.

Peter Drucker describes this changed role as meaning that governments can no longer control the 'weather', they can only control the 'climate'.[1]

Controlling the economic climate so as to promote sustainable growth is a key government responsibility.

It involves more savings and investment, exporting more, revitalising our infrastructure, and increasing our productivity and competitiveness in a host of ways. It also means making sure that the tax and regulatory regimes enhance rather than impede our performance in all these areas.

GOVERNMENTS TO INVEST IN ECONOMIC AND INTELLECTUAL INFRASTRUCTURE

- As part of their actions to positively effect the 'climate' of the economy, governments must now give priority to those areas where they can do most to create the conditions for prosperity.
- Ensuring that we have the infrastructure and human resources to underpin the competitiveness of our front line firms is one such area.

I agree with Gary Sturgess when he writes that in a global economy, the greatest leverage for nationally based governments is found in their investment in public infrastructure (economic infrastructure) and people (intellectual infrastructure).[2]

The challenge for a country as vast and thinly populated as Australia is not only to renew our basic infrastructure—roads, railways, ports, water, sewerage and drainage systems—but to keep up with city-states such as Singapore in laying down advanced infrastructure—optical fibre, satellite transponders and the like.[3]

We also need to go beyond this, and develop a more sophisticated view of the type of infrastructure we need. It's not just a question of roads, railways, and other physical assets which must be efficient; nor is it just a question of putting the newer types of infrastructure such as the super-highway into place. Getting the right systems, or the right software, to make them work is equally crucial.

Let me give you an example of what I mean. Perhaps we're all tired of hearing that our waterfront is inefficient, and maybe we're more anxious to hear some constructive ideas on how to fix it. I believe the solution is not just in labour practices, or the efficiency of cranes or other materials handling equipment, or the physical railway/road connections. Perhaps the solution lies in more effective systems linking the physical infrastructure and the labour practices.

So if an importer wants to bring some piece of machinery through the wharves, we can set up an electronic data system which eliminates much of the customs and sales tax paperwork, and gets it done in a timely fashion, and streamlines the unloading process. The information systems are part of the infrastructure and also need to be efficient.

- Providing infrastructure at world class levels demands that we look at how we currently allocate resources to the provision of infrastructure. Equally importantly, we need to look ahead 10–15 years to identify how the public and private sectors can work together to meet Australia's likely needs.

Despite its extraordinary importance, there has been a long term decline in government investment in infrastructure over the last 35 years from just under 8% of GDP to a touch over 4%. Over the same period, private sector capital investment has fluctuated with the business cycle, but is currently running at the same level as it was at the beginning of the period, approximately 16% of GDP.[4]

If we continue to wonder why the level of unemployment in Australia rises after each recession, we may find some of the answers in our continuing indifference to infrastructure. The stakes could not be higher, nor could the rewards if we are prepared to re-order our priorities.

In part, this means that spending must be redirected from recurrent expenditure to capital expenditure, but the issue is much larger than one of reordering priorities.

In the first instance, we must better allocate our investment dollars. In the road area for example, as EPAC has observed, it can be argued that too much money has been put into minor urban and rural roads, while needs for upgraded arterial roads and highways have been left unmet. The key to overcoming such problems is to adopt a national infrastructure strategy that focuses on getting good projects delivered efficiently.[5] The National Transport Planning Taskforce report completed last year might be the basis of such a strategy.[6]

INFRASTRUCTURE—GET THE PRIVATE SECTOR INVOLVED

We should also get the private sector more involved.

- The private sector lives by the capacity to take calculated risks, but the current tax and regulatory regime does reduce enthusiasm for greater involvement by companies such as BHP. A recent example of this was the Very Fast Train project, which was not viable without changes to the tax regime.
- It should not surprise us that the tax regime is an issue—it was established when governments provided the infrastructure.
- It is not beyond our capacity to remedy these problems and thus open the way for greater involvement by the private sector.
- Greater private sector involvement can bring many benefits: it can help to ensure that worthwhile infrastructure projects are undertaken, and can increase both the quality and quantity of infrastructure.[7] Whatever one's view of the ideology pursued by Mrs Thatcher, there is no denying the tremendous improvement in investment in infrastructure in the UK.

- Private sector involvement also enables Australian business to access world-competitive infrastructure, and can increase employment and growth.
- I would also argue that government investment is inherently less efficient than private infrastructure investment because it reflects a range of non-economic pressures in allocating resources. We have seen this in road funding allocations, over-expenditure on power generation especially in New South Wales, and misapplication of funding for domestic airport infrastructure. Private sector decisions are governed by the need to get a sufficient return on investment, which is a spur to maximising efficiency.

REVITALISING OUR INTELLECTUAL INFRASTRUCTURE

- We need to complement the revitalisation of our economic infrastructure with the renewal of our intellectual infrastructure.

Clearly knowledge is a valuable resource. As a result we are witnessing a struggle by companies around the world for access to knowledge—knowledge personified by a highly skilled and adaptable workforce. In turn, governments are trying to provide knowledge through a system of lifetime training and education in an effort to ensure that they can attract to their country the 'high end jobs'.

While great efforts have been made to improve the accessibility of education, particularly higher education for Australians, I think we have overlooked some vital 'quality' issues.

There is much argument about what constitutes quality, so the definition that I choose is one that was provided by the Senate Standing Committee on Employment, Education and Training several years ago: quality is—'fitness for purpose'.[8]

We live in an age when the pace of discovery of new knowledge is so great as to be overwhelming. The formal knowledge gained, even at the highest levels of learning, has an ever diminishing 'intellectual half-life'.

Technological change may well make people's jobs obsolete several times over before they retire, therefore it becomes critically important that our schools and universities impart the skills and attitudes that prepare employees for a lifetime of learning.

A great breadth of attitudes is also important. Today's workplace increasingly requires engineers, accountants or marketers with language skills, an openness to other cultures and various

other attributes. For example, it is quite possible that a person who joins BHP will find themselves working quite early in their careers in Indonesia, or in Zimbabwe, or in Chile or in the United States, and then in another of these places.

Allied to the skills which will enable people to live and work confidently in other cultures, we need other generic qualities which universities have been very good at providing — things such as intellectual curiosity, problem solving, independent thought, effective communication and the ability to work in a team.

It is the combination of these generic skills with a practical vocational edge that we need to develop within young Australians if they are to get the 'high end' jobs in the global workplace of today.

The third area I want to discuss tonight is developing initiative.

INITIATIVES BY THE PRIVATE SECTOR

- If we expect governments to face up to the realities of our time, so must others — none more so than business.
- While governments must create the environment for prosperity, it is up to the private sector to create the new jobs and the new industries that will enable us to become leaders in the global economy.

A CULTURE OF CONTINUOUS INITIATIVE

- To do that well, I believe we need a culture of continuous initiative in Australia. Rather than casting around for ways in which we can catch up to the dynamic economies of the world, we should be the standard bearers — as we were earlier in our history, when the world looked to us for advances in agricultural and mining technology as well as some social and political concepts.
- I said at the beginning of my speech that achieving prosperity and rising standards of living requires a partnership between government and business. I am not thinking of a formal or legalistic partnership, but one which involves both groups in continuous effort to achieve similar goals; one which is based on shared assumptions about the way we can build on our strengths to improve national living standards.
- Above all, the partnership must be based on a shared vision of Australia's potential, and a recognition that innovation is the key to unlock and add to that potential.
- The Australian Manufacturing Council has put considerable effort into understanding how

innovation works in the broad sense, and three critically important areas have emerged:

> there is the need for world class knowledge infrastructure, involving education, common business practice and an understanding of how the economy and particular industries function;

> the second is the need to forge stronger linkages between industry and its Research and Development providers, its leading edge customers and suppliers, and other firms and networks;

> the third element is the need to significantly improve the internal capabilities of firms.

- All of these elements are connected; improvement in one area alone is insufficient if we want to become a nation of self-starters.

THE DRIVERS OF INNOVATION

- The need for developing a culture of continuous initiative is urgent — a fact which becomes apparent if we look at many of the major issues confronting us. Rather than feeling despondent about the difficulties, we should turn these challenges into the drivers of innovation.

Let me illustrate the point with a few examples.

Given our current account difficulties, increased exports are now crucial to our national well-being.

- Our high value manufacturers and service providers have shown it is possible to crack the toughest overseas markets. We have much more to do in these areas, but why not put our export focus at the centre of all our endeavours? In the case of manufacturers, this would mean investing in or developing the most advanced technologies. For governments, it would mean applying the 'export test' to every policy and every action. If an action obstructed our capacity to export, then the behaviour would have to change.

Our proximity to Asia is a major advantage.

- But timing is important — if we don't build on this advantage, others will establish a presence there and we will again follow in their wake. So we could apply 'strengthening our presence in Asia' as a test at a firm, a government and a community level. Actions which worked against that major national imperative would need to be turned around.

The information superhighway is another example.

- The relevant technologies and concepts shaping this development are changing quickly. Right now, we have an opportunity to get in at an

early stage; that means firms need to explore the business possibilities, and governments need to ensure a competitive communications technology climate. They also need to ask the key question: will these actions that are being proposed work for or against this Imperative? They then need to respond accordingly.

THE ROLE OF BUSINESS IN ACHIEVING A CULTURE OF INITIATIVE

I would like to elaborate on the key role of companies in developing this culture of initiative in their daily operations.

- In essence, the leadership task is to develop and reinforce the culture which drives the company. It means unlocking the tremendous productive and innovative capacity in the workforce. It means finding the motivational triggers for world class performance. For big firms such as BHP, it means rediscovering the fire and hunger for success which saw them transformed from small to large companies.
- Above all, it comes down to commitment and drive and a determination to be the best.
- Already there are many Australian companies and business people showing us the way. Studies that have been carried out by the Australian Manufacturing Council and the Australian Best Practice Demonstration Program hold valuable lessons for the private sector in general.

In simple terms, Best Practice is a tool which helps to instil a culture of initiative aimed at continuous improvement of a business.

- Under the banner of Best Practice, there is a cultural revolution underway in many Australian companies, but many more of us need to embrace that process of change.
- First and foremost — these leading companies, incidentally many of which are of a modest size, have a 'culture of leadership'.
- From the CEO to the individual employee at the sharp end of economic competition, these businesses understand that a strong business must constantly grow both revenues and profits: increasing revenue through a constant stream of new ideas and product innovations and increasing profits through unceasing improvements in productivity. Neither innovation nor productivity alone is enough. A winning company has to master both.[9]
- In traditional firms, ideas are imposed on employees from above. This has the corrosive effect of turning concepts into rules, stripping them of their vitality. Employees change their behaviour, but not their minds. In a leadership

culture, behaviour changes, because minds have embraced change.

- To gain competitive advantage in the future, organisations will need to harness and unleash the creativity and competitive spirit that resides within their people. In practical terms, that means embracing top technologies, providing training and career development, and strengthening the networks which are vital to innovation.

RELATIONSHIPS AND THE 'VALUE DELIVERY CHAIN'

Networks and relationships are a critical source of competitive advantage today.

- Business in the 1990s is far removed from the old notion of 'make a product and sell it'.
- In the truest sense of the expression, every company is now part of a 'value delivery chain' with the greatest rewards going to those companies that provide the highest value to their customers. Within the value delivery chain, every company has suppliers and customers. We need to work relentlessly with our customers and suppliers to see how we can provide a better product and service.
- The same active sense of partnership needs to be developed with all our research and development partners, with unions and with governments.

A culture of innovation and initiative is equally relevant to government organisations. They too need to look at continually improving their operations and harnessing the drive of their people. At a general level, they need to ensure they have the infrastructure and systems and policies in place to achieve the best outcomes for Australia.

CONCLUSION

Ladies and gentlemen, I am an optimist by conviction. I believe that the capacity of people for creativity and change is endless. I am also an optimist by experience. My time in BHP has convinced me that cultural transformation and unlocking potential is possible.

Rather than being anxious about living within a globalised economy, through our ingenuity and reason, Australians can revitalise our country so that our future can be one filled with opportunity and prosperity.

The global convergence of technology, information and markets means the central metaphor of our era is 'connectedness'; those companies — and countries — that turn their linkages into competitive advantages will prosper.

Government and the private sector must be partners in this endeavour if our people are to live with a sense of confidence and poise.

Two centuries ago Adam Smith gave a prescription for national development. Even as we approach the 21st century, the essence of his observation holds true. If I may paraphrase him,

'Little else is required to carry a state to the highest level of opulence ... but peace, easy taxes, investment in a peoples' intellectual development, world class infrastructure ... all the rest being brought about by the natural order of things, foremost being the vitality and drive of the private sector to create superior goods and services.'

I think the assumption behind that prescription is one of partnership. If government and business can work in harmony, growth and the fruits of growth will be ours for the picking.

Thank you.

---

[1] Peter F. Drucker, 'Managing for the Future', Butterworth/Heineman Ltd, UK, 1992, p. 7.

[2] Gary Sturgess, 'Can governments add value in a borderless world?', Sixth National Business Summit, 8–9 March 1995, p. 4.

[3] Ibid, p. 13.

[4] Max Walsh, 'Real picture is in Statement No. 2' in *The Sydney Morning Herald*, 11 May 1995, p. 33.

[5] EPAC, Private Infrastructure Task Force — Interim Report, May 1995, p. 1.

[6] Building for the job: A Strategy for Australia's Transport Network, National Transport Planning Taskforce, December 1994.

[7] 'Impediments to private sector infrastructure involvement', submission by the Business Council of Australia to the Economic Planning Advisory Commission, February 1995, p. 1.

[8] The Senate Standing Committee on Employment, Education and Training, 'Priorities for reform in higher education', June 1990, p. 3.

[9] Noel M. Tichy and Stratford Sherman, 'Control your destiny or someone else will', published Harper Business 1994, p. 20.

JOHN BARRY PRESCOTT

BComm (Industrial Relations) University of New South Wales

SUMMARY

John Prescott is Managing Director and Chief Executive Officer of BHP. He commenced with BHP 37 years ago as an industrial relations trainee and progressed through various industrial relations positions in the Company's Steel and Transport businesses in Newcastle, Sydney and Whyalla before being appointed to line management as Assistant Manager Fleet Operations in 1974. He later became General Manager Transport of BHP in 1982, Chief Executive Officer of BHP Steel in 1987, a Director of BHP in 1988 and was appointed to his present position in May 1991.

He has served on various industry and government bodies and has been closely involved in the reform and reconstruction of the maritime and manufacturing industries in Australia. He is Chairman of the Australian Manufacturing Council, a Board Member of the Business Council of Australia, Patron of the Australian Quality Council, Member of the International Advisory Board of Booz, Allen & Hamilton Inc., Member of the International Council of J. P. Morgan; Member Asia Pacific Advisory Committee of The New York Stock Exchange; and Member Board of The Walter & Eliza Hall Institute of Medical Research.

May 1995.

SYMPOSIUM ON SCIENCE POLICY

The Symposium was held on the afternoon and evening of 25 May 1995 in the hall of the
Royal Society of Victoria, 9 Victoria Street, Melbourne 3000

CONTENTS

PREFACE

Australia is different. We are an outpost of
Western (i.e. Greco–Roman-based) thought and
cultural values in the East. We are also an outpost
of Western-European-style government, wages and
social services—although in population terms, a
very small outpost—in the world's most dynamic
economic region.

However, Australia is not Europe transplanted.
Our OECD-level living standard is not based on
a century of industrialisation and infrastructure-
building. Our wealth is not generated from the sale
of a wide range of competitively-priced manu-
factured goods into a large adjacent market of
high individual spending power.

Instead, we have many of the attributes and
deficiencies of a developing country. In particular,
the basis of our economy is the earnings from our
renewable (food and fibre) and non-renewable
(energy and minerals) commodity exports.

However, there is a pervasive problem faced by
Australia, and by the other resource-providers out
in the Third World. We have an unabated need
for capital inflow from the developed nations of
the First World; but the terms of our trade with
them continue to erode, and thus so does our
ability to sustain the resultant financing charges.

Over a period of decades, the prices achieved
for our wheat and wool have declined in real

terms. Energy is now cheaper, in real terms, than it was in 1974. The break-up of the Soviet Union, the return of South Africa to the world community, and the rise of market economies in the Third World are all making easier the access by explorer/developers to world-class minerals deposits outside resource-rich Australia.

Productivity in our resource industries is generally at a world-class level. To the extent our commodity exports can't compete at times of low prices, the reasons often relate to market distortions outside our control — export subsidies by our competitors, and consumer subsidies — or various tariff and non-tariff import restrictions — by our potential customers.

Ours is still a good country in which to live. Compelling evidence of this fact is that people want to come here and share our culture, our form of government, and of course our wage-levels and social services. Some have risked their lives to get here.

However, Australia is not paying its way in the world.

Our current account deficit continues to grow at an alarming rate (by 6% of GDP in 1994–95) and, despite patently living beyond our means, we still cannot provide sufficient jobs for those who want to work.

Australia is being out-competed in this competitive world.

We clearly have long-term problems as a nation, and long-term solutions are needed.

Our commodity industries provide wealth rather than jobs. If we are to repair our balance of payments position, and if we are to provide intellectually and economically rewarding jobs in sufficient quantity to meet the needs of our children and our immigrants, we must look to other sectors of the economy — manufacturing and services.

Long-term productivity growth in the non-commodity sectors of Australia's economy is below 2% p.a. This is far too low if Australia is to pay its way *vis a vis* the rest of the world, and if it is to protect and enhance its exceptional quality of life. Gone are the days when the sheep's back will carry us.

Obviously there is no quick, easy, or even single, solution to problems which have been creeping up on us for decades. However, productivity is certainly part of the equation. Whether in terms of turning around our widening trade deficit in manufactured goods, or of lifting our foreign earnings from the services sector, science and technology can and must play an increasing role in accelerating Australia's productivity growth, and hence improving our international competitiveness.

There is more to it than just asserting that the Federal Government 'should' provide more money for research at this time of increasing budget stringency; or that industry 'should' transfer a larger share of profits from potential dividends to its R&D budgets; or that more of the top students 'should' choose science or engineering rather than medicine or law.

As Victoria's oldest learned society, the Royal Society of Victoria decided to stimulate thinking among opinion-formers in the community about what must be done. Our field is science, and we decided to make our contribution by assembling the outstanding leaders on science policy for this Symposium.

Unless one is assured of perpetual youth — and infinite wealth — life becomes a series of workable compromises. Your Society found it no less so with this Symposium.

In order to attract the best brains in the Victorian community as an audience, it was crucial that we won acceptances from the speakers whom we felt really could make an authoritative and worthwhile contribution to our topic. As you can see from the program, we got our speakers — but at a price. As you might expect, those we invited to speak were busy people with great demands on their time. We felt unable to insist that their acceptance required the submission of any written material, before or after the Symposium.

This is the reason that these Transactions contain an introduction, three fully-written-out papers, one full paper in note form and one summary. No written material is available from the other two speakers, and the event was not tape-recorded. In our opinion, the remaining talks (two of the more trenchant addresses) were sufficiently important that a lasting record was demanded. They are each represented here by an 'impression' written by one who heard the talks. This is a compromise between our desired objective of publishing the speakers' own written record, and the alternative of providing nothing.

PROFESSOR JOHN M. SWAN FAA

OPENING REMARKS

Why is science policy important? Let me give you two quotations, both from the 17th Century.

'He that will not apply new remedies must expect new evils.'
                              Francis Bacon

The most valuable new remedies, in my opinion, will be those based on scientific investigation and

scientific understanding. Our science policies are important because they will dictate our strategies, our action plans for the necessary scientific research.

'Where there is much to learn, there of necessity will be much argument, much writing, many opinions; for opinion in good men is but knowledge in the making.' *John Milton*

At this meeting we shall hear opinion from good men and good women. And let us remember that even if the opinions are diverse, all of us are trying, from different perspectives, to put in place the most useful and productive science policies for our countries.

Can I suggest, as a basis for this meeting, that good science policies are our lifeline to the future.

Let me give two examples of the importance of science policies. The world population continues to expand; human numbers now challenge the ecological sustainability of the planet. 'Farming in the future' (and I quote from Derek Tribe's recent book *Feeding and Greening the World*) 'must aim to increase productivity while minimising the use of scarce resources such as fossil fuel energy, water, capital and land, maximising the use of plentiful resources such as human labour, solar energy, genetic biodiversity and expanding knowledge, and avoiding the contamination, degradation or destruction of the natural environment'.

Good husbandry on the farm within these constraints, will require more and better scientific understanding of plants and animals, soil, water, nutrients, plant and animal health, the harvesting and transport of crops, down-stream processing, food preservation, marketing.

Effective science policies to ensure that the necessary work is done are essential for achieving this goal of increased agricultural production.

Without good science policies, who will ensure that the required scientists and their scientific knowledge are available to the farmer when needed?

My second example is simply a list, but an astonishingly wide list, of the sciences which are critical to the modern food processing industries. These are:

Biopolymer science;
Bio-organic chemistry;
Crystallisation;
Failure mechanics;
Preservation;
Plant cell technology;
Process engineering;
Rheology;

Colloid science;
Nutrition;
Microbial cell biology;
Fluid dynamics;
Molecular modelling; and
Heat and mass transfer modelling.

The food industry will never compete internationally unless all these sciences and technologies are kept alive and well through good science policies which recognise their importance.

Good science policies really are our lifeline to the future.

Where do the scientists themselves fit in? Scientists often expect:

- a high degree of freedom from bureaucratic regulation and interference;
- open communication via international publication;
- close cooperation between institutions and individuals;

and many scientists also request and sometimes demand,

- a major role in determining the direction of their own research.

The tensions between the autonomy of the research scientist and the degree to which programs can or should be formulated by end users, or influenced by the political process, seem to lie at the heart of much that has been happening in science policy in Australia and New Zealand in recent years. I expect that the papers in this afternoon's session will address these and related issues, and now call on our speakers to take the floor.

SIR ARVI PARBO AC FTS

SCIENCE AND TECHNOLOGY AND AUSTRALIA'S FUTURE

I am delighted to be invited to participate in this Symposium on Science Policy and I warmly commend the Royal Society of Victoria for organising it. You have assembled a very distinguished group of speakers and I am honoured to have been included.

The Royal Society of Victoria has an impressive record in promoting the advancement of science and its application for the benefit of the people of Victoria. I am pleased to be a member and to have been associated with some of the activities of the Society and the former Sciences Club over the years. Indeed, as I recall, Professor Adrienne

Clarke and Sir Gustav Nossal, who are also speakers at this Symposium, and I between us delivered three successive J. E. Cummins Orations from 1990 to 1992.

When I spoke to the Society in 1991, my topic was 'The Changing Earth'. As a miner, that is a subject I have grown up with and know well. I do not profess to be anywhere near as familiar with science policy, but as the recently elected President of the Australian Academy of Technological Sciences and Engineering I am, through necessity, on a crash course of learning fast!

The Academy's role

The main object of the Australian Academy of Technological Sciences and Engineering (ATS) is, and I quote:

'To promote, in the interest of Australia, the application of scientific and engineering knowledge to practical purposes.'

In the field of science and science policy we are therefore at the applied end and include technology. We believe that the practical application of science is essential to our national well-being, and that technological progress, applied in a sustainable manner, is necessary to improve the life of Australians.

If I was to be limited in my comments today to science policy only, I would not feel competent to speak here. With your permission, I would therefore like to include technology and tell you a little about what we in the ATS believe Australia should be doing, and what we in our Academy are doing to help realise the potential benefits of science and technology for the Australian community.

Some questions

Clearly, I cannot in the course of this short address deal with the whole wide field of the place of science and technology in the society. Let me therefore focus on the following questions:

- Do we need a national science (and technology) policy, and what do we mean by it?
- How do we develop community understanding and appreciation of the value of science and technology?
- Can the scientific and technological communities work together in support of national goals?
- How do we develop an innovative culture?
- How do we resolve issues such as the balance between pure and applied research?

- How do we get our best young people to take up careers in science and technology?
- Are we providing the right kind of education in science and technology?

National science and technology policy

Both ends of the political spectrum, science funders, science practitioners, science users, and, indeed, many members of the public, seem to be very much in favour of having a national science policy. At the technology end, the Institution of Engineers, Australia and our Academy in 1992 jointly published a proposal for a national technology policy: copies are available at this Symposium. The joint covering letter by the two Presidents was headed: 'We Must Have A National Technology Policy'.

Such views have been held for a long time. One might then reasonably ask why we don't have such policies or, at least, why many people believe that we don't have them.

The answer seems to lie in the difficulty in defining what we mean by a national science and technology policy. It seems to mean different things to different people:

- To some, it is a national blueprint for setting priorities either within the entire national scientific and technological effort, or within the major sectors of national activity, be they various industries or various disciplines.
- To others, it is simply about defining the best funding arrangements for research.
- To still others, it is about the balance between fundamental and applied research, the mechanisms for capturing for society the benefits from scientific work, attracting the best young people into scientific careers, the arrangements for scientific education, and so on.

Clearly, a national policy must include elements of all these, and more. And clearly also, all these matters are linked with so many other aspects of society that it would be very difficult indeed to produce one all-encompassing document that would stand the test of time in a rapidly changing world. But in casting around for ways to begin, it seems to me that the absolutely essential basis for a national policy is a clear understanding by the decision makers in the community, supported by the community, that science and technology, properly and sustainably applied, is the foundation on which our present and future well-being depends.

When this awareness exists, the other policy aspects follow naturally and can be modified from time to time as required by changing circumstances. Without such understanding, the efforts to formulate a comprehensive policy cannot be successful.

In this context the study under way by Australian Science and Technology Council (ASTEC) entitled *Matching Science and Technology to Future Needs: 2010* could well be a major step ahead in the quest to establish a basis for a national policy. I am delighted to represent the Academy on the Reference Group for this study.

The seesaw

As it is at present, I have to say that I do not think that such a basic community understanding generally exists in Australia today. The high standing of science and technology in the immediate post-Sputnik era has given way to a sense of disillusionment, if not outright hostility.

Professor Geoffrey Blainey, in his book *The Great Seesaw*, identifies a tendency for community beliefs and attitudes to shift and tilt like the movements of a seesaw. He characterises the two extreme positions of society as 'love of nature' and 'love of technology'. He notes that societies wax and wane between these two extremes over time, and that a reversion to nature typically follows a period of frustration with the benefits of technology.

You may recall, as an example, the 'back to nature' movement identified with Jean Jacques Rousseau at the end of the 18th century, which held up the way of life of the 'noble savage' as the ideal. (I understand that Rousseau himself never met a savage in his life, but this did not stop him from pontificating about them. There are parallels here with some of our popular gurus today.)

But Professor Blainey's analysis also concludes that, although technological progress can and does cause problems, it will also help to bring about their solution. No one with even a cursory understanding of how greatly the human condition has been improved by science and technology in the last two hundred years can be in any doubt about this.

Let me give you an important example.

The greatest problem facing the world today is the rapid growth in the world's population. This is the result of the decreasing infantile death rate, the increasing lifespan which in developed economies has doubled in the last 200 years, and the general improvement in the human condition brought about by the revolutionary scientific and industrial progress. Medical science has virtually eliminated the plagues and illnesses which kept the human numbers down until quite recently.

Today we note that the population growth is high in areas where the standards of living are low. Countries with high living standards have negligible population growth. This indicates the likely solution to the problem: as the standards in the rest of the world improve, it can be expected that the growth will slow down and eventually perhaps even reach a plateau. Science and technology, which, because of their beneficial effects to humanity, have caused the problem, are also the key to its solution. Certainly other measures tried so far do not appear to have any chance of success.

Developing community understanding

Why are there doubts about the value of science and technology in the community?

Those of us active in this area tend to assume that the value of what we are doing must be surely self-evident, while various groups in the community have found it useful for gaining publicity, and therefore influence, to concentrate on the real or imaginary ill effects of scientific and technological progress. Such groups, not always constrained by the truth, have been very skilful in capturing the attention of the media with colourful actions and stories and have had a far greater influence on public opinion than the 'quiet achievers'.

We need to become much more active in telling the people in simple words and in an interesting, personalised, and understandable way just how science and technology is benefiting them, and how the adverse side effects of such progress can and are being managed. The current worldwide emphasis on sustainability is now a welcome and essential part of scientific and technological activity. It must provide the answers to the questions which are quite legitimately asked.

We must insist, at all times, on the highest standards of moral and scientific integrity and responsibility in everything we do. Equally importantly, however, we must also tell the public about this.

The point is made very clearly by a verse from a 1914 Broadway play which I happened to see the other day:

The codfish lays ten thousand eggs,
The humble hen lays one;
The codfish never cackles
To tell us what she's done
So we scorn the codfish
While the humble hen we prize.

Recently a new national organisation, Australian Science Communicators (ASC), has been formed, with Julian Cribb as the inaugural President. Its purpose is to bring about broader political and public awareness of the role and contribution of science and technology to our society, its progress, and prosperity. ASC has offered to assist those active in this field in communicating with the public. I believe that this is exactly the kind of development we have been looking for.

We at ATS propose to work closely with Australian Science Communicators and I urge others to do so also. The Royal Society may well decide to take a hand in this.

Powerful new tools for disseminating information such as Internet, home pages, and bulletin boards are now widely in use. The President of the Royal Society, Dr Max Lay, also happens to be the Chairman of our Academy's Technological Information Committee. Perhaps there are opportunities for working together in this area?

A partnership between science and technology

In a recent article the President of The Institution of Engineers, Australia, Dr Ian Mair, said, amongst other things:

'For too long, the engineering work force has been content to leave the leadership of the country to the political process. This process has failed to imbue ordinary Australians with a confidence in their abilities. We live for the present, spending $105 for every $100 we earn as a nation. This is not sustainable.
'We can wait no longer. The Council of the Institution of Engineers has endorsed public-interest issues that it will be joining debate on this year. The issues include public infra-structure, water resources, health, the environment, and information technology. Other issues to be addressed will be the innovation process and engineering education.'

I believe that The Institution is showing the kind of leadership that is needed and I welcome this as a Fellow of the Institution, as well as on behalf of our Academy. The Institution will have our full cooperation in areas in which we are competent, particularly as we are the Academy

of Technological Sciences and Engineering and some one third of our Fellows are also Fellows of The Institution of Engineers. We have worked together in the past — I have mentioned the proposal for a National Technology policy — and we look forward to doing so even more actively in the future.

Similarly, we offer our cooperation to other scientific and professional bodies. We already consult regularly with our sister Academies of Science, Social Sciences, and Humanities through the Consultative Committee of Australian Academies. We were recently pleased to be associated with the Academy of Science and the Academy of the Social Sciences in a major review of Climate Change Science, with many organisations, including the Institution of Engineers, participating on the Steering Committee.

The boundaries between science and technology have always been unclear and are rapidly becoming more so. More than that, science, technology, and the social sciences are beginning to overlap. We do not believe that there are any reasons for rivalries between organisations in these areas, and that there is every reason for full cooperation in the interests of Australia.

An innovative culture

My predecessor as President of ATS, Sir Rupert Myers, often stressed that our greatest need in Australia is to develop and foster a spirit and culture of enterprise. He recently wrote:

'Australians have a history of adopting new technological hardware in their everyday lives. We are among the quickest in the world to buy new gadgets for our home and for our transport, communication, education, and recreation needs. We take pride, too, in seeing Australians discover new scientific things and ideas. We are, alas, not so quick or adept at translating those discoveries into profitable enterprise.
'There is a need to harness our positive attributes to foster an enthusiasm for enterprise and innovation. We need to persuade the young, and others, that it is worthy and admirable to have ideas for making and doing things and then to be enterprising by bringing together skills, materials and methods for doing this profitably and for the benefit of consumers and the community. It is worthy to become an entrepreneur and not just an employee.'

I agree completely with Sir Rupert and I hope that we all, The Royal Society, the Academies, professional bodies, other organisations, and we all as individuals, will do all we can to help introduce this culture into Australia. ATS is delighted that the Minister for Industry, Science and Technology, Senator Peter Cook, is at present leading a major Federal Government campaign in this area and we are pleased to assist in this.

Balance between pure and applied research

One of the perennial issues in debate is the balance of effort and resources between so-called 'pure' or 'basic' and 'applied' research, between 'research' and 'development', between 'R&D' considered generically and 'commercialisation', or 'application'. It is frequently asserted, and I have no reason to differ with this observation, that Australia is doing well in research but that, when it comes to capturing the economic benefits of that research, we do not do nearly so well.

The ATS has repeatedly and consistently argued the need for a greater effort in this area, and I agree wholeheartedly. This is a task which, like so many others in the commercial world, is never 'done': there is always room to improve, to do better, to exceed our previous best. I would not, however, like this to be taken to mean that our record in commercial applications is wholly poor, or that we should not strive to maintain our proud national record in basic research.

I believe that our rural industries have been remarkably successful in making practical use of our research achievements in this area. I know from personal knowledge that in the minerals industry we have been equally successful in building linkages between the research community and industry. We have excellent communications with the Universities, the CSIRO, the former Bureau of Mineral Resources (now the Australian Geological Survey Organisation), and some particularly effective cooperative interface mechanisms such as the Australian Mineral Industries Research Association (AMIRA). When mineral and petroleum exploration is included as research—which it is—the industry is not only spending heavily on research, but can show excellent returns from this spending.

It is relevant to note that three of the four recipients of this year's Australia Prize in the field of remote sensing were supported in their prize-winning work by companies in the Australian mineral industry. I am proud to say that one of the winners was a Fellow of our Academy.

But the benefits from research do not occur only in the industrial sector. There are fields in the public domain where our record is up with the best in the world. For example, Australia's achievements in weather and climate research and in oceanography and hydrology and the translation of that research into benefits to the national economy is outstanding.

Turning now to the balance between basic and applied research, I know that there is much concern in the scientific community that the recent emphasis on immediately useable science may be putting at risk what some, at least, see as one of our real sources of competitive advantage, namely our longstanding tradition of excellence in basic research. I understand that these issues got a public airing recently during the visit to Australia by the editor of *Nature*, Sir John Maddox, who has become increasingly vocal in supporting continued commitment to basic research in the UK.

I cannot visualise that anyone would seriously argue that Australia should not do any basic research. The debate can be only about the proportion of the total effort that goes into either area. Is it too simplistic to say that the effort going into applied science must be such that it enables the economy to grow at a satisfactory rate, thus making more total resources available and therefore more for both basic and applied research? To put it the other way, if our economy does not grow sufficiently, less will be available for research of any kind.

May I be permitted another simplistic question? Because it is so difficult to define better measures, we generally use the funding available as the criterion of the adequacy or otherwise of the research effort. But surely what matters is not how much we spend, but what we produce. What really matters is not the funding, but the results from the funding. Is it possible to develop measures of the output, rather than of the input?

I am sure that others today, more knowledgeable in these matters than I, will pursue this topic further. Our view in ATS is, that it is a very important issue, that both basic and applied research are essential to our future, and that any decisions on the balance between them should be made on a rational and objective basis.

Attracting young people into science and technology

Encouraging our best young people to take up careers in science and technology is in my view closely related to creating better public awareness

and understanding of the role and importance of such activities to the community. If science and technology are high in public esteem, young people will want to be involved. If they are not highly regarded, it is understandable that young people will seek careers in other areas. The points made earlier under the heading 'Developing Community Understanding' are therefore directly relevant here.

Initiatives such as the Australia Prize, established by the former Minister for Science and a Fellow of our Academy, the Hon. Barry Jones, are very valuable in this context.

Education for science and technology

While not an expert, I have heard enough informed comment on this topic to be convinced that there is no uniquely 'right' model for education and training in this area.

Science and technology have not been attracting large numbers of high quality students and there have been suggestions of increasing pressures to modify the rigorousness of the courses to maintain enrolments. If true, this would be a matter for very serious concern. We need more rigorous, not less rigorous, training to meet the demands of the future.

A major review of engineering education is about to commence, conducted jointly by the Institution of Engineers, Australia, as the professional and accrediting body, the Australian Council of Engineering Deans, and the Australian Academy of Technological Sciences and Engineering. It is to report in 15 months. Similar reviews have been previously conducted in other areas. Jointly, their conclusions must form an important part of any national science and technology policy.

The Academy

Let me conclude by commenting further on the Academy of Technological Sciences and Engineering.

Established in 1975, its 470-odd Fellows come from all branches of technological sciences and engineering and represent the top achievers from academia, government, and industry in their fields. Their work on behalf of the Academy is on a voluntary basis through a number of Committees, Task Forces, and Study Teams of Fellows and others. There are Divisions of the Academy in all States.

We are frequently asked to express our views on various matters within our competence which are under review or study by the Federal government. We conduct symposia and seminars on issues of particular interest. Standing Committees include Education for Technological Sciences and Engineering, International Relations, Technological Information and Sustainable Development.

We undertake major projects of study and inquiry; time prevents me from elaborating on these. Some of these projects have been mentioned earlier. The report on the most recent study on Climate Change is available at this Symposium. Please take one and read it. It has been widely distributed in Australia and overseas, including to all secondary schools and municipal libraries in Australia. It is an authoritative, impartial, and objective summary of the present scientific understanding and the uncertainties in this very important issue.

One ongoing Academy project which has been very successfully operated for more than five years and has been extended for a further five years is the Crawford Fund for International Agricultural Research, which enables professionals from Australia and from other countries, mainly in Asia, to learn about the agricultural practices and technology developed in Australia, and to form linkages between Australian and overseas agricultural professionals and organisations. Added to it this year has been similar training in biotechnology. The activities of the Fund are highly recognised internationally and supported by the Australian Government and private industry.

But the international dimension of the Academy's work extends further.

The Academy is a founding member of the Council of Academies of Engineering and Technological Sciences (CAETS) which links together 15 like Academies, so far mainly in Europe and North America. This provides valuable links to technological developments in these areas. The International Relations Committee conducts bilateral programmes with like Academies in countries in our region. Thus, for example, we have active exchange programmes, involving workshops, in targeted areas with China, Korea, and Taiwan (the latter two in association with the Australian Academy of Science). We are developing links with Indonesia, Thailand, Malaysia, and the Philippines and are assisting in the formation of like Academies where these do not currently exist. We believe the benefits of scientific and technological exchanges are mutual and often lead to commercial linkages.

Conclusion

I hope that these brief observations and the wilful addition of technology to your topic of science

policy have been of some value. I regret that a commitment in Sydney this evening prevents me from participating fully in this Symposium, but let me assure you that this is not because of lack of interest. I look forward to hearing in due course about the conclusions.

Allow me once again to assure you of the full cooperation of the Academy of Technological Sciences and Engineering in any areas which lie within our competence.

Professor Adrienne E. Clarke ao fts faa

SCIENCE, TECHNOLOGY AND AUSTRALIA'S FUTURE

1. Science Policy in Relation to our National Goals

Achieving a strong capability in S&T is a necessary, but not sufficient, part of a strategy for achieving our National goals, which fall into three groups:

- economic prosperity;[1]
- environmental welfare; and
- social, cultural and welfare issues.

Indeed, innovation—particularly technological innovation—is widely viewed as a key driver of the economic prosperity of nations. At this time in the history of the world, science is pervasive in human affairs.

Economic prosperity

Economic prosperity is a goal not only of the business groups; it is acknowledged as important by many environmentalists, and at least by inference by welfare organisations who see the destructiveness of unemployment and inadequate resources.

Looking ahead to 2020 it is likely that the main bases of wealth creation will be in:

- resource-based industries;
- high value-added manufacturing and services industries; and
- new knowledge-based and information-intensive industries.

Our science and technology capabilities, underpinned by our standards of education and training, will be crucially important to success in all these areas. Increasingly our goods and services are differentiated by their S&T content.

Environmental welfare

We must be careful, much more careful than in the past, to prevent economic activity destroying our air, polluting our water or damaging our genetic resources. We have to protect, indeed restore, productivity of our soils. Our quality of life certainly includes visual and environmental amenity. We have a wonderfully diverse biota in Australia, which we must conserve for our own profit and pleasure and for that of future generations.

Again science and technology is absolutely critical to achieving an improved environment. As we establish more knowledge about our ecosystems, we are better able to achieve higher levels of sustainable development. Our overall welfare will not be improved by negative, zero, or even slower rates of economic growth.

Social, cultural and welfare issues

Our lives are being radically changed by the revolution in media and information technology. Information and capacity for education will, within a short time, become more generally accessible, and there will be a variety of new means for cultural expression and communication. The creative potential being unleashed by such things as new technologies at the theatre and by new materials in the plastic arts is quite staggering. In the health sciences the contribution of science and technology to the relief of human suffering, extension of life and improved quality of life for the handicapped is evident in many families.

It is critically important that we care for the less fortunate members of society by spreading wealth through the taxation and then the welfare system. This requires that we generate sufficient wealth to spread.

- Policy issues centre on long term planning to attract investment—to capture our share of global wealth.
    This includes:
    1. Maintaining and enhancing our long-term capability in S&T.
    2. Learning to capture the value from our investment in S&T.

2. Factors to Consider in Formulating Tactics for Implementing a Strategy of Maintaining a Strong Capability in S&T

Many Australians, including many of our decision-makers, have a very hazy idea of what

S&T really is—public education is critically important.

Australians often do not recognise that all our everyday goods and services have a strong S&T content. Just think of the technology involved in the local supermarket: getting the goods grown or produced, the scheduling and inventory control to keep the shelves full, the electronic scanning at the checkout counter and the amazing EFTPOS technology. We tend to take all this for granted, as we do the fact that clean water comes out of taps and the sewage somehow disappears. Most people do not realise that behind our clean water and our sewage system is an excellent capability in microbiology, in chemistry and in engineering and other technologies. Someone, somewhere has sat at a desk or a laboratory bench and written the software or designed the tests and someone owns the technology. As a nation we tend to have a cargo cult mentality—the technology is simply there when we need it. We are pleased that the recent racehorse mystery deaths were traced to a virus, without really understanding what a scientific feat the exercise was or grasping the importance of the knowledge behind solving the mystery. Thinking more broadly, managing the global challenges facing the world, for example, problems such as population control, AIDS, the Greenhouse effect, ozone depletion, pollution and wastage disposal, all require a strong knowledge base in science and technology.

• Policy issue is the education of all Australians, especially the next generation, in S&T. We must be a technology-literate nation.

  What is knowledge? Again many people have a hazy idea of the nature of knowledge.

Two main forms of knowledge are handled routinely by scientists and they feed off each other:

(i) Established knowledge—this can be organised with a series of 'rules' which allow automation. For example, we have automated tests for the AIDS virus—in blood samples: someone will own the knowledge embodied in the test. This knowledge can be licensed or sold or traded really more or less as any other goods or services. There will be a standard operating procedure or protocol for the tests and the confidence limits for these measurements are known.

(ii) Evolving knowledge—this is less certain and is the knowledge generated by research. It too can be protected and traded. In fields such as biotechnology, this type of knowledge is heavily traded. Our experience in Australia, in handling the trading and commercialisation of this knowledge, is limited, but we are improving.

We live in the borderless world

We now live in the 'borderless world' where raw materials, capital, information and technology can be bought and moved quite easily. One of the important differentiating features of Nations, and of cities, is the skills and inventiveness of their people. A workforce with a capability for doing complex things attracts investment. (A good infrastructure for communication and transport makes a skilled workforce even more attractive; a competitive taxation and regulatory environment is also essential for putting together a competitive bid *vis a vis* other countries, for global investment opportunities.)

International capital migrates to attractive environments for R&D, and access to technology for sophisticated manufacturing or it migrates to low cost labour. We will not (at least at present), and would not want, to attract capital because of our low cost labour. We must attract capital for other reasons; one compelling reason will be the strength of our S&T base.

Economic growth is being driven by new technologies and their applications. Winning companies put together the best research, engineering, design, manufacturing and distribution wherever they can get it anywhere in the world. Winning countries must provide the infrastructure, education, research, and accessible capital so that winning companies will want to carry out as much value-added activity as possible in these countries.

Our past economic performance

In his book *The End of Certainty*, Paul Kelly[2] quotes,

'In 1870 ... income per head was then 75% higher in Australia than in America. By the end of the 1920s Australia had dropped to fourth place; by 1980, to 11th. On recent performance Singapore will overtake Australia within 10 years followed by Malaysia, Taiwan and South Korea within a generation.'

Since this comment we have continued to slide to 16th or 17th place despite our considerable natural advantages. No wonder this has focused attention of the Business Council of Australia on league table goal setting. Kelly continues,

'Australia was the only industrialised nation that failed to increase its proportion of exports to GDP over the 30 years from 1960. This period saw the greatest expansion of wealth in human history, driven by the expansion of world trade, but Australia participated as a half member, not a full member ...

'... Australia's transition to sustained economic progress is sure to be a lengthy and turbulent process.'

3. The Importance of the Nation's Skill Base in S&T

Countries that aspire to high living standards, and consequently high returns for labour must stay at the cutting edge of science and technology in enough specialisations to make that possible.
Robert Reich[3] makes this point,

'First: The standard of living of a nation's people increasingly depends on what they contribute to the world economy — on the value of their skills and insights ... Second: The skills involved in problem-solving, problem identifying, and strategic brokering improve with experience ... Together, the two points suggest a simple truth. A foreign-owned firm ... that contracts with Americans to solve or identify complex problems helps Americans far more than does an American-owned firm that contracts with foreigners to do the same.'

Science and technology is less tangible at airports, harbours, power and communication systems than in products and services, but no less important. In the economists' terms[4] science and technology has huge 'spill-over' benefits for society when used properly and calls for a mix of private and public sector financial support. (Indeed, measuring 'spill-over' benefits from S&T has become a whole new occupation for economists.)
A case can be made on the basis of international comparisons that Australia at both the level of government and business is under-investing in science and technology.

While international comparisons are fraught with difficulties, the commitment to science and technology being made by the Asian 'Tigers' is a clear pointer to the importance these countries place on increasing their expenditure on S&T to the levels of leading OECD countries. Their efforts will inevitably influence the competitive environment in which Australian companies will find themselves in the not so distant future.

If Australia sees its closer integration into the Asian-Pacific economic community as being vital to its future, and if we wish to be one of the nations that contributes to developments and has the capacity to respond to them flexibly, being willing to invest in S&T and innovation is essential.

The Asian 'Tigers' are not thinking in a time frame coincident with the next election. They are thinking in terms of generations. Because capability in S&T is not acquired quickly, we must also get into the mind set of long term strategic thinking for the benefit of Australia and future generations.

Whether we like it or not, Australia is in a global competition where relative capability in S&T will to a large extent determine economic performance. Investment in S&T and the associated education and skill capabilities are of great importance to society and a long-term investment.

No country, and certainly not one the size of Australia, can realistically expect to be self-sufficient in terms of R&D. We need balance between generating innovations internally and adapting innovations developed elsewhere. The more closely our scientists and technologists are connected to their counterparts elsewhere, the more possibilities we will have for developing strategic alliances. (Remember, we only generate 2% of the world's new knowledge!)

The policy issues that arise from this discussion are the same as those set out earlier:

1. Maintain and enhance our long term capability in S&T.
2. Learn to capture the value from our investment in S&T.

with the addition of a third point

3. Build our international connections for S&T. This requires that we are very good at what we do and can therefore win a 'seat' at the international table and form alliances which are beneficial to Australia.

4. The Intellectual Capital of the Nation — Our Greatest Asset

Understanding our intellectual capital

The accounting profession has developed an approach to describe the knowledge content of a business[5]. We can be sure that once the accounting profession takes an interest in these matters, there is money in it. This is a good reason to take the whole business very seriously. They talk about intellectual capital, being the sum of the human capital, the structural capital and the customer capital.

Just as companies looking to the future now rank intellectual capital as their most valuable asset, so too can intellectual capital be considered as Australia's most valuable asset for forging our future.

Intellectual capital is the sum of the intangible assets of knowledge, skill and information. For a business the intellectual capital is a sum of:

Human capital
  — the individual skills required to meet a need
Structural capital
  — the organisational capabilities required to deliver to a market need
Customer capital
  — the strength of its franchise, its brand name, how the company is valued by its customers

Human capital — the people

Human capital is the source of innovation and renewal of the system. It is the people who know about a subject. The people who know about viruses, computer programs, eucalypts, and bilbies. People who understand physical chemistry, such as how fluids such as molten chocolate, molten gold, oil and red mud flow and so on. People who understand how to clone genes and transfer them. People who can design and build complex machines. People who in short know about the things we need to know.

Certainly we have a record of producing Nobel Laureates and a steady supply of first class scientists whose skills are in demand in the world. They are trained initially in the Universities as graduate students. These leading scientists are now found within CSIRO, the Universities and the Research Institutes. They move throughout the world; they are welcomed to the top labs, both industrial and public sector labs, because they have something special to offer, something that few others have — really leading edge knowledge, which is extremely valuable. They have a very good idea of what is going on in the world in their field and personally know all the main players. These are the people who set the directions for research in Australia and set the standards for the next generation to aspire to. Is our supply of first class scientists adequate? Are we creating an adequate environment for these people to flourish? What is our succession plan? How attractive is a career in science compared with law, medicine and accountancy? My perception is that attempts to create a proper research career for scientists within the Fellowship Scheme of the Australian Research Council are not being consolidated. We need to do much more to create predictable and attractive career paths for our young scientists.

• Policy issue is to make career paths in S&T attractive to the brightest and best of young Australians.

Structural capital

Structural capital comprises the information systems, knowledge of markets and customers and expertise in all parts of the chain that turn individual 'know-how' into property.

This is again a problem for Australia. The scientists do not have specialist knowledge of the markets and lack experience in the commercialisation of new knowledge. We have few people in business skilled in the arts of identifying, protecting and commercialising technology. The key to realising on our intellectual capital is to bring the leading researchers together with knowledge-users in industry and create a class of business-literate scientists. (It is much harder to create science-literate business people if they have no technical language.) This is being done very effectively in some of the CRCs. Indeed the CRC scheme is probably the most important event in science policy in Australia since the creation of the CSIRO. In particular the CRCs can offer the graduate students some training in aspects of business practice. Some will be very interested, others will prefer to focus on scientific skills; however, by offering the opportunity, we will start to broaden the horizons of some of our scientists. Constructing financial incentives linked to the benefit of their contribution to a business for scientists is worth considering. This might be considered equivalent to share option schemes for motivating senior executives in business. Scientists need and deserve adequate compensation for their creativity.

• Policy issue is the reward and incentive packages for scientists involved in the commercialisation of science.

However, one of our most difficult problems is the fact that we have so few companies with an in-house R&D capacity. That is, there are few companies in Australia who have people who can speak the language of science, and recognise the opportunities for adding value or developing new products from scientific knowledge. It has been estimated that there are only 50 companies with in-house R&D capacity. If we subtract the cohort of mining companies from this group we are not left with much. Fortunately we see the emergence of the SMEs which are firmly based in technology.

One of our tactics must be to create an environment in which these companies can flourish. We should consider schemes in which scientists from both CSIRO and the Universities, can take intellectual property and 'have a go' at developing it, perhaps with leave of absence for three years and access to start-up funds. As the SMEs are our fastest growing source of growth of employment and they are all technology-based, it makes sense. Similar schemes are working well in the USA — why not here?

Customer capital

The customer capital is the value customers put on the enterprise, how they interact with the organisation to give feedback to both the human and structural capital.

In National terms this is how Australia is perceived in the world. Are we a good place for investment in the borderless world? Can we deliver on S&T? Do we have a technologically literate work force? Are the other issues of cost of transport, taxation environment, cost of utilities etc competitive?

It is critically important that we attract that investment and through the investment grow the intellectual capital of the country; we therefore have to ensure that all these items which go into making an investment decision are competitive.

5. CSIRO's Role in a Changing World

CSIRO plays a crucial role in enhancing Australia's competitiveness. It houses a significant part of the Nation's intellectual capital. It employs 3000 scientists and engineers in all disciplines; it has laboratories in over 100 sites across Australia. It manages some of our finest National facilities, for example the Australia Telescope, which is currently being leased by an American team to search for extraterrestrial intelligence; the Animal Health Laboratories at Geelong which played a key role in diagnosing and managing the recent outbreak of morbillivirus in racehorses in Queensland; and two of Australia's research vessels, the *RV Franklin* which has undertaken oceanographic research all round the Australian coastline and is important in work on climate variability and the *Southern Surveyor*, the fisheries research vessel, which is helping to resolve issues relating to sustainable management of our fisheries resources.

Another facility which is of major national importance is the National Standards Laboratory which sets the primary standards for physical measurement for Australia. Those standards underpin many aspects of our daily lives, such as weights and measures and measurement of time. A high proportion of the total resources of the Organisation are directed to problems and opportunities related to the environment and agriculture, and a significant proportion are directed to various aspects of the manufacturing industry.

Formally the role of the Organisation is laid down in the Science and Industry Act and in the Ministerial guidelines issued to CSIRO by the former Minister for Science, Barry Jones, in June 1988. In practical terms, CSIRO is in the business of strategic research focused on achieving specific outcomes for the economic, environmental and social benefit of Australia. This requires a mix of research from basic and long term to tactical and short term; the particular mix will vary over time and across the Organisation. For example, many of the projects undertaken in the field of mathematics and statistics will have time lines of months compared with time lines of many years for projects directed to environmental problems. Optimising the mix obviously requires careful planning, which is dependent on the knowledge and foresight of the research leaders within CSIRO. It is very important that in this planning our reservoir of knowledge, that is our intellectual capital, is continually replenished. The Organisation must maintain its level of scientific excellence. The level and nature of the contract work which it undertakes is a consequence of this planning.

This life as a world-class strategic research organisation, focused on specific outputs is a change from its pre 1987 life as a science-driven organisation. It is a change which has been embraced with more or less enthusiasm and commitment by different parts of the Organisation. During Dr John Stocker's tenure as CE the process of change was started; it is continuing during Dr Roy Green's tenure. The Organisation has evolved into flexible groups doing excellent innovative work for their customers, which includes the Australian community. Of course change is difficult and uncomfortable and it is not surprising that there is a vocal minority who are resistant, but this all has to be put in the context in the world in which we live. Australia is in a state of change and many organisations within Australia are in a state of change. Science and technology organisations around the world are also having to accommodate to stakeholders who demand more technology to be delivered more efficiently. Governments are recognising the importance of S&T as key components of National competitive-

ness and as a knowledge base for policy formulation, and are looking for ways of improving their return on investment.

One aspect of the change many R&D organisations are coming to grips with is change from being performers of research to being providers of science and technology for specific groups of customers. An important aspect of the change relates to the global village concept — R&D laboratories are in a competitive market place; customers for S&T will buy their product from wherever it is available within the world — the best product at the best price. Australia's strength in S&T is a powerful attraction for investment of multinational companies in their R&D facilities. Investment captured in turn enhances our National intellectual capital.

The CSIRO is part of this change in R&D organisations world wide, it is competing in the global marketplace and it competes extremely effectively in many areas. But the change from a large 'university without students' to an outcomes-oriented provider of S&T has lead to some clashes of past management culture with the new directions. The past culture was biased to achieving high scientific status and personal ambition; the results were measured mainly as published research articles. While the Organisation will always require scientific excellence as the foundation for its activities, additional achievement measures of customer satisfaction, of team performance, and of delivery of contracts on time and on budget are becoming the norm.

Of course there is resistance to change. The forms of resistance follow the classic patterns defined from studies of large organisations in change. These patterns of resistance are quite predictable. First there are the defence routines expressed by individuals — Don't hear messages; deny that the message applies or rationalise that leaders don't understand[6]. Next there are the classic features of the transition culture marked by 'certain individuals expressing fierce criticism and rejection, with others vigorously supporting the new values and vision'. Robert Gottliebsen[7] put it very well in relation to resistance to change in the Australian context by another group in change, the educators.

'Many ... know what must be done, but too many are devoted to the lifestyle and aspirations of the 1970s and do not realise the world has moved on. They will fight with all their energy to resist change and they will enlist the support of the friends they have in the media.'

It does seem that in many S&T organisations there are a number of factors which create exceptionally high levels of resistance to change. This surprised me; I had imagined that because scientists are commonly dealing with changing ideas and concepts that they would adapt easily to change. The normal resistance is believed to be compounded by a factor related to the education of researchers. The background to this is the fact that scientists specialise and focus on sets of specific skills and knowledge. They are thus committed to particular long term directions and find it very difficult to come to grips with major changes in direction[8]. This is compounded by a narrow experience and lack of understanding of the language commonly used in the worlds that now impact on S&T, the worlds of business, of the law and of government. And, of course, scientists almost by definition tend to be strongly individualistic.

Ultimately, however, the success of change in an organisation is dependent on the behaviour of individuals within the organisation. The CSIRO is fortunate to have within its ranks a large cohort of exceptional people who are successfully and creatively producing the required outcomes for Australia. Eventually others will be brought into the new era or will find an environment more suitable to their needs. It will take time. Like other organisations, the CSIRO had made mistakes in its management of change. Like other organisations, with the benefit of hindsight we may well have done some things differently. However just as the patterns of resistance are predictable, so are the mistakes large organisations in change make.

From a study of 100 organisations in change Kotter[9] draws two general conclusions.

'Firstly, that most successful corporate change efforts go through a series of phases that in total require a considerable length of time. The second general lesson is that critical mistakes in any of the phases can have a devastating effect, slowing momentum and negating hard won gains.'

He concludes that even the most successful change efforts are messy. However, for CSIRO, the change process is being accepted and accepted with enthusiasm, by most of the Organisation. Our scientists are thinkers and doers and are committed to the success of the Organisation in serving Australia.

6. CSIRO's Response to the Industry Commission Inquiry into R&D

CSIRO welcomes two important aspects of the Industry Commission's draft report:

- its acknowledgment of importance of R&D to Australia's economy, an issue neglected in mainstream economic debate in Australia; and
- its recognition that R&D is complex and offers a wide range of benefits, many of which cannot be predicted.

However, CSIRO is concerned that the Commission's policy proposals place too much emphasis on segmentation of R&D stages and roles, including a clear public/private sector demarcation.

The Commission has recommended that CSIRO's principal role should be 'public good' research. We consider this role to be too narrow to ensure the maximum return on Australia's investment in CSIRO research. To constrain CSIRO to this role, even with the addition of some full-cost contractual research, would have the effect of isolating the Organisation from many of its clients. Rather, we believe CSIRO's role should be seen in terms of national benefit—that is, research in the interests of Australia, which allows a variety of relationships with industry and other users and the flexibility to meet changing demands.

The Organisation has a history of delivering value to the Nation. It is adapting and learning to operate in changed circumstances. It is a key resource for our future competitiveness and for many aspects of National security, for example, our biological security. We would argue for a wider role than the strict public good role and look forward to playing our part in forging Australia's future.

PROFESSOR IAN LOWE

(one listener's impression of his talk)

ONE LEG EACH SIDE OF THE BARB-WIRE FENCE: SCIENCE IN MODERN AUSTRALIA

Why should we do science in Australia? It is to:

- understand the world in terms of techniques, data and theories;
- make a cultural contribution to the world of which we are a part;
- engender innovation and subsequent commercial developments;
- produce skilled and educated people;
- keep our most able people in Australia; and
- pay our 'dues', and thus earn 'a seat at the table' of international science.

Those who have a scientific mind-set are useful to Australia in all areas of human activity, such as in the collection and refinement of data and in the testing of theories ('mindless economic nonsense' was given as an example) against the real world.

The situation in 1995 is that Australia has demonstrated an ability to do good basic science. However we have run into problems now that we expect those same scientists to commercialise their knowledge.

R&D by business enterprises is in better shape than a decade ago because of Government's 150% tax deduction. Overall, Australia's proportion of GDP going into science and technology is greater than in similar-sized OECD counties such as Canada, Italy and Austria, but below that of South Korea and Taiwan.

Success in harnessing the efforts of CSIRO and universities to the pursuit of innovation will

[1] Clarke, A. E. (1989). Resources for Science and Technology and their Utilisation. Paper presented at the First Meeting of the Prime Minister's Science Council, 6 October, pp. 41–69.

[2] Kelly, P. (1992). The End of Certainty, published by Allen & Unwin.

[3] Reich, R. (1991). Work of Nations: A Blueprint for the Future, Simon & Schuster, p. 154.

[4] Dowrick, S. (1994). The Role of R&D Growth: A Survey of the New Theory and Evidence. Paper commissioned by the Industry Commission for its Inquiry into Research and Development. Industry Commission, June 1994.

[5] Stewart, T. A. (1994). Your companies most valuable asset: intellectual capital. Fortune 130 No. 7, pp. 34–36.

[6] Shein, E. (1992). How can organisations learn faster? The problem of entering the green room. Invited address to the World Economic Forum, Davos, Switzerland.

[7] Gottliebsen, R. (1995). Blueprint for management change. Business Review Weekly, May, pp. 6–8.

[8] Clark, J. B. (1994). Cultural change in a national research organisation in times of extreme turbulence. Elsevier Science BV, pp. 143–166.

[9] Kotter, J. P. (1995). Leading Change: Why Transformation Efforts Fail. Harvard Business Review, March–April, pp. 59–67.

continue to be mixed, although the best CRCs are likely to be big successes. Some parts of CSIRO will be unable to adapt to a fee-for-service world.

There is a problem in young peoples' perception of science. For twenty years now the best and the brightest at matriculation have chosen not to go into Science at university. Med is as boring as ever but kids still choose it — they even need higher scores for Phys-Ed than for Science. Kids don't see Science as the adventure of new knowledge — but as the memorising of old knowledge. The way we teach persuades young people that science is boring.

Government is pre-occupied with the clever country, economic miracles and setting priorities; and it sees science as a servant to these ends. (Churchill said 'science should be on tap, not on top'.) We can define Australia in the context of:

• the structure and emphasis of the economy;
• a small domestic market;
• our long distance from larger (overseas) markets;
• our small influence in international markets;
• subsidies for our primary industries (e.g. irrigation dams);
• other incentives/disincentives influencing the economy:
• the scale and ownership of corporations in Australia;
• our industrial relations tradition;
• the barriers faced by Australia's manufactured exports cf. the (lesser) barriers faced by imports to this country;
• ideological zealotry (e.g. Industry Commission).

Australia's science policy agenda needs to contain:

• a commitment to basic science, in terms of both funding and jobs;
• a balanced portfolio of R&D, including basic science and product innovation at an appropriate scale;
• policies for innovation including tax incentives, Government coordination, purchasing policies, export incentives and import replacement incentives; and above all
• a contextualising vision.

In support of the need for a vision — if we don't know what sort of Australia we want, any science policy will do. It is a pity Australia stopped the $½ million/year it spent on the Commission for the Future.

The private sector aims particularly at process, rather than product, innovation; and this leads to a problem. Process research to reduce labour and material costs also reduces jobs — and therefore the work force sees it as threatening.

Although Government spending on science as a whole has remained stable over the past decade in real terms, the proportion spent on medical research has doubled. When Government says it can't afford to fund something, it is a statement of priorities not of absolutes.

Every other special interest pushes its case in Canberra for more money. Barry Jones, former Science Minister, describes scientists as 'wimpy lobbyists'. (His draft national technology strategy failed to win funding, although it still reads very well today.) Any group seeking to win a point will select its evidence — but in science, the word populariser' is a term of abuse!

Dr Laurie Hammond

(one listener's impression of his talk)

NO NEED FOR LESSONS:
THE IDEAS ARE CONTAGIOUS

New Zealand's Foundation for Research, Science and Technology dispenses an annual budget of $NZ310 on behalf of Government. However, our speaker resisted the call to provide 'lessons' from New Zealand science policy which might be applied in Australia. 'No one likes advice from little brother.'

In New Zealand, something had to be done. Prior to the reforms of the past five years, Government spending on S&T had declined 27% in real terms in the space of a decade.

The major elements of the reforms to date are as follows:

• There is now a clear split between S&T policy (the prerogative of Government)/the research purchaser (his own organisation)/and the research provider (universities and research institutes). This split has clarified the role of Government — as the formulator of policy.
• The new arrangements ensure both contestability in the provision of research (at least in theory, anyone can apply to do research in New Zealand) and full pricing for the successful research-provider (gone are the days of block funding, or of supplementary funding at the margins — research institutes therefore must re-capitalise from retained earnings).
• Government now provides a selective allocation of resources in line with its current S&T policy.

Its priorities are reflected in the dollars provided for individual R&D sectors, and this process ensures a continual 'rebalancing of the national research portfolio' to reflect future needs — not past expenditure patterns. Some continuity is inherent in the methodology, because sectoral funding strategies are on a five-year rolling basis.

- There has been an organisational restructuring of those who supply the science. DSIR is no more. A series of Crown research institutes has been erected in its stead; and it will be their individual responsibilities to remain viable. (This restructuring is more significant in the NZ context than would be the case here, because universities and industry provide proportionately only half as much research as in Australia. One of Government's aims is to use its funding to leverage-up the low level of business investment.)

The reform process continues. Over the next five years, an effort will be made to:

- Get the long-term strategic framework right. It is the intention to develop a 15-year planning horizon supplemented by 5-year priority statements. There will be no change in the 5-year funding limit.
- Evaluate investments. Different areas of policy interest will need to be allocated different levels of funding; and different evaluation methods will need to be developed to assess the economic/social/environmental outcomes of past funding initiatives.
- Shift the focus to the demand side. Less emphasis will be given to science policy and more to technology policy.

The Minister cannot direct the placement of funds — only enunciate priorities. All Government funding is distributed through contracts with the Foundation for Research, Science and Technology; and these contracts are for a maximum of five years — although longer-term horizons can be enunciated. Basic research has survived, despite fears at the outset.

Clearly, the reinvention of government in New Zealand (accountability/labour and finance reform/corporatisation/privatisation) has led to the reinvention of the science funding system.

The problem in Australia is the lack of a strategic view for science. Without that, we cannot have a science policy. Some see Australia's pluralistic Federal/State system as not requiring a policy for science. But all countries need answers to the questions: Why invest?/In what?/What is the required outcome?

There are those thinking about the topic here. The Industry Commission has canvassed the concept of contestable funding for CSIRO — although is that feasible if research funding for others is not contestable?

The Senate has attacked CSIRO for moving funding between topic areas; but the Senate sees funding 'in terms of the pork-barrel, not science priorities'. Federally, policy ideas tend to originate outside Government *per se*, largely in CSIRO. At the State level, research is handled within the bureaucracy — but science in general is a 'basket case' in the State system.

Returning now to New Zealand, the benefits flowing from the new ways of handling science policy and allocating research funds are several:

- Government confidence in science has been restored;
- sustained growth in science funding is assured — probably for 15 years;
- science has been able to escape history and embrace the future; and
- imperatives for user uptake and investment have been created. (There must be a commitment from the private sector in an area for it to attract increased funding.)

Finally, the lessons of the new way are:

- direct and comprehensive funding means that bad science, and that without priority, has nowhere to hide;
- Government thinks better when it is a strategic investor and shareholder;
- treasury-driven simple-mindedness is avoided; and
- selective investment helps to avoid short-termism and 'safe science'.

PROFESSOR MICHAEL PITMAN OBE FAA

SCIENCE POLICY: LOOKING FORWARD

Summary

Science policy is not static but needs to evolve as the context for using science changes and as different issues need to be addressed. The past year has been marked by a number of studies or consultations such as the IC Report, the ASTEC foresight study, CSIRO's futures papers and the lead up to the Innovation Statement due later this year. These consultations have collected a range of views on current policy and how it might develop.

ASTEC has had a major study in progress on Foresight or *Matching Science and Technology to Future Needs*. This study has suggested scenarios in 2010 as imaginary — but possible futures in order to ask when developments might take place in science and technology and what issues might become most important.

The study is conducting a series of 'Partnerships' in a number of areas such as the information and communications industry, shipping, urban water supply and health. ASTEC is also seeking the views of youth. It is also conducting roundtable discussions on key issues. One took place on 24 May in Sydney on the science system of the future.

ASTEC's scenario for 2010 challenged the discussion by proposing that by this time the use of Internet and communications technology had produced many changes in learning. Universities were internationally open and students could shop around for courses. It was suggested that research had also become more international and multi-disciplinary using Internet; CSIRO had become an international agency (a proposition that attracted some interest from the press); industry carried out more R&D but Government support for R&D had stayed about the same in real terms as now, making funding more competitive and linked more tightly to the Governments needs, such as the environment.

New technologies and discovery in medicine had responded to the search for prevention rather than cure. There are, of course, other futures.

The aim of these discussions is not to predict the future but to use optional futures to challenge the extent that the present system can adapt to trends that can already be detected, such as the role of information technology, the emergence of APEC and importance given to environmental values.

My aim today is to challenge thinking about science policy — both policy for science and science for policy by emphasising that policy — or strategy — needs to take the context of the future into account.

Mr Peter J. Laver fts

AN INDUSTRY EVALUATION OF AUSTRALIAN SCIENCE POLICY

The place of Science Policy

• Science Policy is *not* an end in itself.

• Science Policy is not research policy — it involves 'buying' new technology as well as 'making' or producing it domestically.
• Science is a component of virtually all government policies:
  — industry;
  — trade;
  — agriculture;
  — health/medical;
  — defence;
  — environment; and
  — social.
• Need to determine where science fits in each.
• Answer is different in each case so a generic 'Science Policy' is not necessarily relevant.

Science Policy — what it is not/should not be

• A focus on inputs
  — Dollars do not equate to quality or effectiveness.
  — Business expenditure should be dictated by industry structure and business plans, not international comparisons (as useful as a policy on garden tools, street cleaning or sporting attendance).
• Balancing public and private outlays
  — Private outlay on science is a business decision based on competing investment opportunities.
  — Public expenditure is a political decision based on competing priorities and the inertia inherent in an existing establishment.
• Picking winners/setting priorities
  — Criteria to be used by those not the users of outcomes are unclear.
  — Business may be stupid or short-sighted but in the end it lives with the consequences.
  — Government has role to consult and co-ordinate public interest science.
• Creating jobs — for scientists, tax specialists, lawyers, accountants, snake-oil salesmen
  — Any policy measure intentionally or unintentionally having a primary impact of this nature should be abandoned.

Science Policy — what it should be

• Creating awareness/interest
  — Community fear or apathy makes political support for science difficult.
  — Attitudes significantly influenced by the school education system.
  — Science lacks the inherent potential for popular acclaim/rewards of other fields of endeavour.
• Reducing risk/leveraging returns
  — Investments of any type are rarely simply 'go'/

'no go' decisions but fall within a spectrum, influenced by both quantitative and empirical factors.

— Science and technology decisions need to compete with other investment opportunities.

— Anything government can do to reduce risk or enhance reward will lift science outlays.

• Providing trained, motivated people

— A component of both awareness raising (attracting more of the right people into science) and of risk reduction (reducing the cost of investment in science).

— Ideally a flexible education system is required, creating lifelong learners responsive to changing demands, more likely to be a product of a government than an industry driven system.

— Links between teaching and research in higher education are invaluable, if not essential.

• Funding the pursuit of knowledge

— Every country needs to devote some resources to expanding human knowledge; richer countries more so than poor countries.

— The amount devoted should be a policy matter, similar to decisions on education, welfare etc.

— Indicators as to quantum can be provided by international comparisons and assessing what the marginal outlay would be.

— Research training is an essential component of pure research activities.

• Addressing market failure

— Government science policy needs to cater for areas where co-operative research efforts can be beneficial but the individual beneficiaries are too small to initiate and manage the work — agriculture is the prime example.

— Public good research where there is no identifiable customer or beneficiary also requires support — climate, environment, most medical research.

— Less clear cut is the need to intervene to support visionary, high quality work in the stage before it can attract venture capital.

Evaluation of current Science Policy features

• Government research laboratories CSIRO/ANSTO etc.

— World class research is done but effectiveness could be improved.

— Meet most of the criteria for basic and public good research but applied research could be managed more flexibly.

— Improvement with more industry direction at Institute level, Institute specific goals,

procedures and policies directed to outcomes and leveraging external contributions.

• Tax concessions/IR&D grants

— These have been seen to be good schemes and highly effective in increasing Business expenditure on research.

— Disappointingly low number of eligible companies are utilising the schemes.

— Of concern is whether for the outlay involved the government is receiving the optimum return on its investment, as some research is being driven by the wrong motives and may not be well managed.

• CRCs and AECs

— Have been demonstrated generally to be highly effective in expanding well managed applied research and leveraging government outlays.

— Competitive basis instrumental in setting national research priorities.

— The system needs to be granted permanent status but also needs mechanisms to reduce centres, re-allocate funds and start new ventures.

• ARC/NH&MRC

— Well respected and managed schemes producing effective basic research.

— Success rate is too low so either funds need to be increased or application criteria tightened.

— Excellence should remain prime criterion but relevance needs to be considered, particularly if there is an associated CRC to benefit from the resulting research training, skills and new basic science.

• Rural research corporations

— Generally meet all criteria and provide effective science underpinning for diverse sectors.

— Emphasis needs to be on market pull, matching industry contributions, technology transfer avenues and balancing longer term strategic needs with shorter term tactical problem solving.

• Science and technology awareness programmes

— A major need exists to increase the pool of talent in science and engineering, to heighten community awareness and support for science and to ensure science and technology is better understood in business (especially financial markets) and government.

— Efforts need to be broadly based but particularly focussed in schools, some existing outlays need to be evaluated e.g. Australia Prize.

• International links

— Policy needs to be handled with caution to ensure it supports rather than replaces or distorts market based initiatives.

—The role should be to act as an identifier of opportunities and broker, not a long term participant.

Conclusion

• Australian Science Policy in general is sound and meets most of the desirable attributes.
• Government outlays on science are substantial and must be continuously monitored to ensure that they are yielding the optimum return for taxpayers.
• Science policy will only be effective when considered as a component of other government policies, as a means to achieving various social and economic objectives. It is not an end in itself.

PROFESSOR SIR GUSTAV NOSSAL AC FRS FAA

AUSTRALIA'S SCIENCE POLICY

The nature of science

Ever since human beings started to cultivate crops in the fertile crescent some 8 millennia ago, and probably long before that, humans have expressed their desire to understand and, if possible, conquer nature. The yearning for greater understanding seems to be buried deeply within human consciousness. The most accurate birthday to assign to the birth of science is the birthday of *Homo sapiens*, which seems to keep fluctuating but at a best guess is about a million years ago. I hold unshakeably to the belief that science is primarily about ideas, is integrally involved with the quest for greater knowledge of the world around us and of ourselves. This being said, it seems undoubted that there was a major acceleration in the activity that we call scientific research stemming from about the time that Galileo died and Newton was born, i.e. the last 300 plus years. Few would deny the proposition that steep acceleration in scientific activity was occasioned by the industrial revolution and two world wars.

Faustian bargains in science

Thus we see that from the dawn of the scientific age there are issues to be faced at the interface of science and technology. Knowledge is desirable and good, but scientific knowledge is somehow categorically different from other sorts of knowledge in that it is vectorial, incrementally verifiable

and ineffably powerful. Scientific insights that brook no contradiction lead to powers that know no limits. It is actually interesting to reflect on the number of occasions that scientists have misread the implications of their own work. Rutherford thought that atomic physics was an interesting intellectual exercise. Marconi thought that wireless would be useful for ship to shore communication. The scientists from Rhone-Poulenc who invented the world's first major drug for the treatment of psychoses thought they were inventing an anti-shivering agent for cardiac surgery. Many scientists who love the world of ideas, who struggle to reach insights before their competitors, have no particular concern for where the discovery might eventually lead humanity.

Science Policy thus a house of cards

This being the case, science policy has to be built on shifting sands. There is a tremendous temptation to force the scientific enterprise into a modality that is technological rather than scientific. There will be a time in the development of any science that the technological and practical spin-offs become obvious. There will also be joyous, intellectually challenging, fascinating and fantastic things requiring to be done within the domain of technology for society to get the maximum dividend from scientific discoveries. Nor is it a simple linear sequence. Frequently, the problems and challenges that emerge as scientists struggle to make breakthroughs from the world of ideas practically useful in the world of human beings and their daily concerns will feed back to the basic scientists undreamt of challenges. An enlightened science policy will take due heed of these imperatives.

Australia's position in science and technology

For reasons that are not easy to discern, the great effort that went into Australian science and technology between the years 1930 and 1980 was somewhat slanted towards the fundamental end of the science and technology spectrum. Starting with CSIRO, moving onto the Australian National University, and finishing with the enormous upsurge of the Australian universities after the Murray Report and Martin's assumption as head of the Australian Universities Commission, we have a situation in Australian research where the basic science end is fantastic, where a certain applied research capacity exists, but where there is a significant lack of recipient vehicles within

Australian industry to derive the maximum advantage for the economic benefit of the nation of indigenous Australian discoveries. Of course, the great exceptions are the primary industries, agriculture and mining.

The last decade's great pendular swing

Progressive recognition that Australia seemed not to be getting sufficient economic, social and environmental benefit from its R&D effort, and that many good opportunities for commercialisation had gone overseas, has engendered over the last decade or so a pendular swing towards research for practical ends. This has been largely, but not entirely, driven by Government policy, including the CRC movement, the 150% tax deductibility for R&D, syndicated R&D schemes, GIRD grants, the 30% external earnings imperative of CSIRO and specialised schemes such as Factor F. Strapped for cash, the academic community has vigorously embraced the new collegiality with the industry sector. In fact, I believe Government is not aware just how far universities in particular have moved. The problem is that the business sector itself has not moved as fast, and recent surveys show the continuation of scepticism about R&D in many business enterprises. Nevertheless, the growth rates of business expenditure on research and development show a heartening trend from a low base.

The risk of swinging too far

As with all pendular swings, the risk is that the change in emphasis may have gone too far. The continuing malaise within CSIRO is just the tip of the iceberg. There is a loud minority view within CSIRO that strategic science has been threatened by recent Board policy. Within the universities, the citation impact studies of Bourke and Butler suggest that we are publishing as much, but that our research may be losing some of its edge. At the coal-face, competition for NH&MRC and ARC grants has never been tougher and among our young people within universities there is a real sense of embattlement. We are giving the wrong signals to young Australians at the very time when, at long last, the rhetoric of both Government and Opposition is placing science, technology and innovation high up on the national agenda. Bodies like the Australian Academy of Science and The Royal Society of Victoria must be prepared to stand up and be counted in insisting for a continued high profile of fundamental research within the nation, because this is, indeed, the crucible from which all applied discoveries emerge.

The danger of talking to ourselves

One problem with the science policy debate in Australia is that we spend a great deal of time and effort in preaching to the converted. We should be working hard as ambassadors for science in our general lives, within our communities, and most particularly with sceptical decision-makers who have not yet become as convinced about the value of R&D as we are ourselves. Foremost among these are the senior economic bureaucrats and business and industry leaders. Interestingly, politicians do seem to have got the message. At the wider community level, education about the importance of scientific principles has to begin as early as possible. The Academy of Science, as well as its traditional interest in secondary school education, is now heavily involved with primary school science education as well. This is long-term work of enormous significance.

Minister Cook's innovation statement

Now that the budget has been brought down, and found to be largely neutral in terms of science and technology development through Government funding, the next major focal point has to be Minister Cook's Innovation Statement. At a recent speech before the Australian Academy of Science, Minister Cook declared that he had so far received little help by way of new ideas from the science community. He described in some detail the difficulty of a Government which does want to sponsor science and technology but finds itself surrounded by advice to get its own spending down. In other words, any new initiative which might be proposed that would cost the Government money would have to be accompanied by suggestions about what spending should be cut. This leaves us with a challenge of tendering advice as to how the Government could spend money 'smarter' rather than just simply spending more money on research and development. One useful outcome of the present symposium might be to float some ideas which could be included in the Innovation Statement. I would undertake to pass these on to the Minister for examination. I intend during my speech to make a few suggestions of my own for what could be in the Innovation Statement.

BIOGRAPHICAL DETAILS FOR SPEAKERS

SIR ARVI PARBO AC FTS

Chairman, Western Mining Corporation
Holdings Limited
President, Australian Academy of Technological
Sciences and Engineering

Sir Arvi Parbo was born in Tallinn, Estonia,
on 10 February 1926, and received his early
education there and in Germany. After attending
the Clausthal Mining Academy in Germany from
1946 to 1948 he emigrated to Australia in 1949.

He married Saima Soots on 4 April 1953, and
has one daughter and two sons.

He graduated from the University of Adelaide
with a Bachelor of Engineering Degree with First
Class Honours in 1955 and is a Chartered Engineer.

Sir Arvi joined Western Mining Corporation as
an Underground Surveyor at Bullfinch, Western
Australia in April 1956, and served as Underground
Manager, Nevoria Mine, from 1958 to 1960.

He held the position of Technical Assistant to
the Managing Director from 1960 to 1964 in
Melbourne, and returned to Western Australia in
1964 as the company's Deputy General Super-
intendent. Returning to Melbourne in February
1968, he was appointed General Manager and
became a Director in September 1970.

He was appointed Deputy Managing Director
in May 1971, and became Managing Director in
November 1971.

In October 1974, Sir Arvi was appointed Chair-
man and Managing Director of Western Mining
Corporation Limited. In June, 1986, he relin-
quished the position of Managing Director and
became executive Chairman. In December 1990,
he retired as an executive but was appointed non-
executive Chairman.

In August 1987, Sir Arvi was appointed a
Director of the Broken Hill Proprietary Company
Limited and was appointed Chairman in May 1989,
until retirement in May 1992.

Sir Arvi was appointed Chairman of Alcoa of
Australia Limited in February 1978, Chairman
of Munich Reinsurance Company of Australia
Limited in May 1984, and Chairman of Zurich
Australian Insurance Group in March 1985. He
is also a Director of the Aluminum Company of
America, Hoechst Australian Investments, and
Sara Lee Corporation, and a Member of the Chase
International Advisory Committee.

In May 1989, Deakin University made Sir Arvi
an Honorary Doctor of Science. In June 1989,
Monash University awarded him an Honorary
Doctor of Engineering, and in August of the same
year, Curtin University of Technology appointed
Sir Arvi an Honorary Doctor of Science. In March
1991, in the Silver Jubilee year of Flinders Uni-
versity, Sir Arvi was appointed an Honorary
Doctor of the University.

He was a made a Knight Bachelor for services
to industry in January 1978, and was awarded
the Commander's Cross of the Order of Merit
of the Federal Republic of Germany in 1979. In
November 1990, Sir Arvi was awarded the Grand
Cordon of the Order of the Sacred Treasure of
His Majesty the Emperor of Japan. On Australia
Day 1991, the National Australia Day Council
honoured Sir Arvi with an award as an Australian
Achiever for 1990. In June 1993, Sir Arvi was
made a Companion of the Order of Australia.

PROFESSOR ADRIENNE E. CLARKE AO FTS FAA

Born in Melbourne in 1938. Professor Adrienne
Clarke was a part-time Member of the former
CSIRO Executive. She became a Member of the
CSIRO Board at its establishment in December
1986. She has been Chairman of CSIRO since
December 1991.

Professor Clarke is Director of the Plant Cell
Biology Research Centre at the University of
Melbourne.

Professor Clarke was appointed Officer in the
General Division of the Order of Australia in
1991. She is a Member of the Scientific Advisory
Board of the Friedrich Meischer Institute (Switzer-
land) and is a Fellow of the Australian Academy
of Technological Sciences and Engineering and
a Fellow of the Australian Academy of Science.

Professor Clarke received her tertiary education
at the University of Melbourne and her post-
doctoral education at Baylor University, Houston
and the University of Michigan, USA. She has
held positions on the academic teaching staff of
the University of Auckland, New Zealand, as
well as the University of Melbourne, where she
was appointed to a personal Chair in Botany in
1985. Her research work has been in the field of
cellular recognition in plants, particularly in inter-
actions controlling fertilisation and pathogenesis.
This field also includes the chemistry of complex
carbohydrates found in plants.

PROFESSOR IAN LOWE

Ian Lowe is a Professor and Head of the School
of Science at Griffith University, where he was
also from 1980 to 1992 Director of the Science
Policy Research Centre. He holds a Bachelor of
Science from the University of New South Wales

and a Doctor of Philosophy from the University of York.

Professor Lowe's principal research interests are in the broad area of policy decisions influencing use of science and technology, especially in the fields of energy and environment. He is the author or the co-author of four books, 10 Open University books, 20 book chapters and more than 300 other publications or conference papers. He also writes regular columns for several publications, as well as contributing frequently to radio and TV programmes.

From 1983 to 1989 Professor Lowe was a member of the National Energy Research, Development and Demonstration Council, chairing its Standing Committee on Social, Economic and Environmental Issues. He spent most of 1988 on secondment from Griffith University as Acting Director of the Commission for the Future. He is a member of the Pulp and Paper Research Board, the Advisory Committee of the Australian Road Research Board, the Queensland government's Alternative Energy Advisory Group and a Working Party reporting to the Australian Science and Technology Council on future research strategies. He is a member of the Steering Committee overseeing the corporatisation of the Queensland electricity industry, a member of the advisory committee constituted by the Minister for Immigration and Ethnic Affairs to prepare the Australian response to the 1994 World Population conference, and a member of the Bureau of Immigration and Population Research Advisory Committee. He chairs the Australian government's State of the Environment Advisory Council and the Queensland Health Promotion Council. He has conducted recent consultancies for all three levels of government.

Professor Lowe is active in a wide range of community groups, especially in the areas of consumer interests and environment issues. He chairs the Queensland Conservation Council and the Queensland Consumers' Association, as well as being Deputy Chair of the Council of the Australian Consumers' Association. At the invitation of the ABC, he delivered the 1991 Boyer Lectures in association with Professor Fay Gale, Vice-Chancellor of the University of Western Australia. Professor Lowe was named Humanist of the Year in 1988.

DR LAURIE HAMMOND

Dr Laurie Hammond's research career has been as a marine ecologist, working in the West Indies, Australia and the Pacific on nearshore and con-
tinental shelf/slope systems, particularly coral reefs. Much of his research was at the interface of biology with chemistry, geology and physical oceanography.

Dr Hammond is now Chief Executive of the Foundation for Research, Science and Technology in New Zealand, as a consequence of his interest in the management of research and, particularly, the management of public investment in research and innovation. New Zealand's bold reform of its public administration is another reason he took his current position, because the restructured New Zealand science system is now undergoing a striking transformation, which includes a commitment from government for major funding growth over the next decade and a half.

The Foundation is the major public funder of research, science and technology in New Zealand, managing ca. \$310 M or about two-thirds of the government's investment through schemes that cover basic research through to industrial innovation. It also provides contestable, independent policy advice, grounded in its day-to-day experience of science providers and users.

In the last few years Dr Hammond has contributed to international debate about management of national research and innovation systems, through interactions with agencies in North America, Europe and Asia. He also retains an involvement in research and scholarship, through studies of science, art and society.

Education:

1990 — Master of Business Administration, University of Melbourne

1979 — Doctor of Philosophy, University of West Indies

1973 — Bachelor of Science (Hons), James Cook University

PROFESSOR MICHAEL G. PITMAN OBE FAA

Current position: Chief Scientist, Department of the Prime Minister and Cabinet

The Chief Scientist provides advice to the Prime Minister and to the Minister Assisting the Prime Minister on Science on issues related to science and technology, and is Executive Officer, and a Member, of the Prime Minister's Science and Engineering Council. The Chief Scientist is Chair of the Coordination Committee on Science and Technology; Chair of the Cooperative Research Centres Committee and a member of the Australian Science and Technology Council.

Michael Pitman was born in Bristol in 1933 and educated at Colston's School, Bristol. He was a scholar at Sidney Sussex College, Cambridge and took Natural Science Tripos with Botany in Part II. He was a Fellow at St John's College from 1959–1962. In 1962 he went to the University of Adelaide as Lecturer in Botany and in 1966 was appointed to the Chair of Biology in Plant Physiology at the University of Sydney, a position he held to 1983 when he was appointed Director of the Institute of Biological Resources in CSIRO. During 1987 he was Deputy to the Chief Executive in CSIRO. He was appointed Chief Science Adviser in the Department of Industry, Technology and Commerce from 1988–1992. He was elected to the Australian Academy of Science in 1981.

He has served on various Boards and Committees concerned with science and technology and with marine science in Australia. He has been Chairman of the Trusts of the Australian Museum and of the Royal Botanical Gardens, Sydney.

Michael Pitman is an Emeritus Professor of the University of Sydney.

MR PETER J. LAVER FTS

Biographical details

Corporate General Manager, External Affairs, Broken Hill Proprietary Co. Ltd

This function involves BHP's corporate Government, Community and Public Affairs, Economic Affairs, International Business and Environmental Affairs.

Previous positions have been:
  Corporate General Manager Technology & Development (1990–1992)
  General Manager Transport (1987–1989)
  General Manager BHP Steel International (1985–1987)
  General Manger Operations—Steel Division (1982–1985)
  General Manger Mt Newman Mining (W.A.) (1981–1982)

(Prior to 1981 Mr Laver held several operational management positions located at various BHP sites.)

Current representations include:
  Chair National Board of Employment, Education and Training
  Chairman—Energy Research & Development Corporation
  Chairman Koppers Australia Pty Ltd

Director:
  Continental Carbon (Australia) Pty Ltd
  Australian Centre for Innovation and International Competitiveness (ACIIC) University of Sydney
  Strategic Industry Research Foundation
  Australian International Education Foundation Council

Member:
  Fellow Australian Academy of Technological Sciences & Engineering
  Fellow Institute of Engineers (Aust)
  Fellow Australian Institute of Mining & Metallurgy
  Member Institute of Metal & Materials (Aust)

Former positions include:
  Council Member Australian Maritime College (1987–1990)
  President Institute of Metals and Materials Australasia Ltd (1988–1989)
  Member Australian Manufacturing Council (1984–1988)
  Chairman Basics Metals Industry Council (1984–1988)
  Director Australia Wool Research & Development Corporation (1990–1993)
  Deputy Chair Australian Science & Technology Council (ASTEC) (1984–1994)

Born in Melbourne 1940, educated at Carey Grammar and Melbourne University, graduating in Metallurgical Engineering. Undertook advanced Management Programme of Harvard University— 1984.

Married, with two daughters.

SIR GUSTAV NOSSAL AC FRS FAA

Gustav Nossal was born in Bad Ischl, Austria, in 1931, and came to Australia with his family in 1939. He studied Medicine at the University of Sydney and, after two years' residency at Royal Prince Alfred Hospital, moved to Melbourne to work as a Research Fellow at the Walter and Eliza Hall Institute of Medical Research, leading to a Doctor of Philosophy Degree. Apart from two years as Assistant Professor of Genetics at Stanford University, one year at the Pasteur Institute in Paris, and one year as a Special Consultant to the World Health Organization, all his research career has been at the Hall Institute, of which he became Director in 1965. He is also Professor of Medical Biology at the University of Melbourne.

Professor Nossal's research is in fundamental immunology, and he has written five books and 460 scientific articles in this and related fields. His eminence in immunology has been recognised by his election as President (1986–1989) of the 25 000-member world body of immunology, the International Union of Immunological Societies. He is also interested in the interface between science and society, well illustrated by his Presidency of the Australian Academy of Science, his last two books *Medical Science and Human Goals* and *Reshaping Life: Key Issues in Genetic Engineering*, and his membership of the Prime Minister's Science and Engineering Council. He was a member of the Board of CSIRO from 1987–1994. As a sign of his commitment to public health and preventive medicine, he is Chairman of the Victorian Health Promotion Foundation. Professor Nossal's work in the field of international health is carried out in collaboration with the World Health Organization, where he chairs the committee overseeing the Global Programme on Vaccines.

Professor Nossal was knighted in 1977 and made a Companion of the Order of Australia in 1989. He has received numerous other honours from Australia, the United Kingdom, the United States, the Federal Republic of Germany, France, India, Austria, Israel, Mexico and Poland. Amongst the most significant are Fellow of The Royal Society of London, Foreign Associate of the US National Academy of Sciences, Member of the Academie des Sciences, France, the Albert Einstein World Award of Science, the Emil von Behring Prize, the Rabbi Shai Shacknai Prize, and 75 named lectureships in nine countries.

Professor Nossal is also involved in charitable work as Chairman of The Felton Bequests' Committee; and in the business community as a Director of CRA Limited.

LIST OF THOSE ATTENDING

Mr Ian Anderson

Professor Warwick Anderson, Baker Medical Research Institute

Ms Kerry Angwin, Business Victoria, Department of Business & Employment

Dr Neil Archbold, Councillor RSV

Dr David Baker-Gabb

Dr Brett Bateup

Dr Tom Biegler, CSIRO

Profesor Herb Bolotin, Department of Physics, Melbourne University

Professor Willem Bouma, CSIRO Division of Atmospheric Research

Dr Bill Briggs, Councillor RSV

Dr David Brockway, CRC Power Generation

Professor A. W. Burgess, Ludwig Institute for Cancer Research

Mr Ken Buxton, Australian Computing & Communications Institute

Dr John Carnie, Manager, Infectious Diseases, Heath Protection Section, Public Health Branch, Department of Health & Community Services

Professor Bill Charters, Dean of Engineering, University of Melbourne

Professor Brian Cherry, Associate Dean, Research & Development, Faculty of Engineering, Monash University

Professor Adrienne Clarke AO FTS FAA, Chairman CSIRO

Professor Paul Clark, Deputy Vice-Chancellor, Victoria University of Technology

Dr Peter Colman, Chief, CSIRO Division of Biomolecular Engineering

Dr Wynford Connick, Director, AMRL

Professor Stella Crossley, Department of Psychology Monash University

Dr Michael Dalling, Managing Director, Strategic Industry Research Foundation

Mr Jerry de la Harpe, Howard Florey Institute, University of Melbourne

Dr Michael Dixon, IBM Australia Limited

Dr Paul Donaghue, Chief Scientist, ICI Australia Technology

Dr Phil Dyson, Centre for Land Protection Research

Mr Robert Edgar, Keith Turnbull Research Institute

Professor R. J. Evans, Department of Electrical Engineering, University of Melbourne

Ms Tania Ewing, *The Age*

Mr Bob Foster, Councillor RSV

Dr Russell Garnsworthy, CRA Ltd

Mr Clyde Garrow, Councillor RSV

Dr Roy Green, Acting Chief Executive, CSIRO

Mr Alain Grossbard, Eastern Energy Ltd

Dr Laurie Hammond, Chief Executive, Foundation for Research, Science & Technology, New Zealand

Mrs Margaret Harris, Councillor RSV

Mr Martin Harris, Managing Director, HBH Technology Industries Pty Ltd

Mr John Haydon, General Manager, Technical Standards Branch, AUSTEL

Professor Thomas Healy, School of Chemistry, University of Melbourne

Dr Rod Hill, CSIRO Division of Mineral Resources

Mr Trevor Hilton, KPMG House

Mr Keith Hoffman, Chief Executive Officer, Powernet

Mr D. S. Humphreys

Ms Jennifer Irving, Department of the Premier & Cabinet

Dr R. W. Jemison, UniMelb Ltd

Dr Martin Jones, Transfield Defence Systems

Professor David Kelly, Dean, Faculty of Science & Technology, La Trobe University

Mr Tony Kjar, Minenco Pty Ltd

Dr Geoffrey Knights FTS

Dr R. D. la Nauze, Chief, CSIRO Division of Minerals

Mr Peter Laver FTS, Corporate General Manager, External Affairs, BHP

Dr Phillip Law AO CBE

Ms Wendy Lawler, Faculty of Science, University of Melbourne

Dr Bruce Livett, Department of Biochemisty & Molecular Biology, University of Melbourne

Professor Ian Lowe, Head, School of Science, Griffith University

Mr A. J. Mackenzie

Dr Michael Manton, Councillor RSV

Professor T. A. McMahon, Department of Civil & Environmental. Engineering., University of Melbourne

Mr Robert Meehan

Dr Graham Mitchell, CSL Limited

Dr Jens Mohr, Hoechst Australia Ltd

Dr Bill Murphy, Councillor RSV

Mr Jim Murray

Dr Mike Murray, Chief, CSIRO Division of Materials Science & Technology

Dr Garth Newman, Fisheries Branch, Department of Conservation & Natural Resources

Mr Pin Ng, Business Victoria, Department of Business & Employment

Ms Jane Niall, Department of the Premier & Cabinet

Professor Ian Nicholls, Department of Earth Sciences, Monash University

Sir Gustav Nossal AC FRS FAA, President, Australian Academy of Science

Mr O. T. O'Flynn

Ms Maureen O'Keefe, Faculty of Science, University of Melbourne

Associate Professor Richard O'Sullivan, Australian Institute of Physics

Dr Frank Papa, Department of Manufacturing Systems Engineering, RMIT

Sir Arvi Parbo AC FTS, President, Australian Academy of Technological Sciences & Engineering

Dr Michael Pitman OBE FAA, Chief Scientist, Department of Prime Minister & Cabinet

Mr Brian Powell, RD, Montech Pty Ltd

H. R. C. Pratt

Professor Ian Rae, Deputy Vice-Chancellor, Victoria University of Technology

Dr Russell Reichelt, Australian Institute of Marine Science

Dr James Reid, Cobden Medical Centre

Mr George Riffkin, Agriculture Victoria

Dr Brian Robinson, Chairman, Environment Protection Authority

Professor Jarlath Ronayne, Vice-Chancellor's Office, Victoria University of Technology

Professor Hyam Rubinstein, Department of Mathematics, University of Melbourne

Associate Professor Gordon Sanson, Councillor RSV

Dr Peter Saunders

Dr Brian Sawford, CSIRO Division of Atmospheric Research

Professor Bill Sawyer, Department of Biochemistry & Molecular Biology, University of Melbourne

Dr Nalin Sharda, Department of Computer Science, Victoria University of Technology

Mr Jim Starkey, Executive Director, Australian Institute of Petroleum

Dr Raymond Steedman, Australian Institute of Marine Science

Ms Ros Stirling, *Australian R&D Review*

Mr David Strong

Mr G. S. Sutherland FIEAust CPEng, Institution of Engineers Australia

Professor John Swan FAA

Mr Philip Thomas, Vanan Australia Ltd

Dr Brian Tucker

Professor Daryl Tucker, Research Director, Faculty of Science & Technology, Deakin University

Mr Peter Voylay, Department of Industry, Science & Technology

Dr R. G. Ward

Professor Jim Warren, Councillor RSV

Dr Graeme Watson, Department of Zoology, University of Melbourne

Mr Eric Webb

Dr Norman Wettenhall

Professor R. E. White, Department of Agriculture, University of Melbourne

Mr W. I. Whitton

Mr Doug Williams

Mr Roger Woodhouse

PROCEEDINGS

OF THE

ROYAL SOCIETY OF VICTORIA

INCLUDING

TRANSACTIONS OF MEETINGS

Volume 108

CONTENTS OF VOLUME 108

DOWNSTREAM HYDROGEOMORPHIC IMPACTS OF EILDON RESERVOIR ON THE MID-GOULBURN RIVER, VICTORIA

Wayne D. Erskine

School of Geography, University of New South Wales, Sydney, New South Wales 2052, Australia

Erskine, W. D., 1996:09:30. Downstream hydrogeomorphic impacts of Eildon Reservoir on the mid-Goulburn River, Victoria. *Proceedings of the Royal Society of Victoria* 108 (1): 1–15. ISSN 0035-9211.

Little Eildon Reservoir (377 450 ML capacity) was built on the Goulburn River between 1915 and 1927 to supply irrigation water to the Goulburn–Murray Irrigation District. To meet increasing demands for irrigation, the larger Big Eildon Reservoir (3 390 100 ML capacity) was built immediately below the original dam between 1950 and 1955. Flow regulation by Little Eildon Reservoir resulted in a non-significant reduction in mean annual runoff; maintenance of the natural seasonal flow distribution despite increasing summer flows and decreasing winter flows; a changed probability distribution of mean daily flows such that high flows were reduced, moderate flows were increased and low flows were reduced in duration; and a decrease in downstream sediment load from 210 000 m³/a to 12 300 m³/a. Flow regulation by Big Eildon Reservoir resulted in a further reduction in mean annual runoff; a totally reversed seasonal flow distribution with maximum flows in summer and autumn and minimum flows in winter and spring; a further change in the probability distribution of mean daily flows which magnified those initiated by Little Eildon Reservoir; lower flood peak discharges for all return periods; and a further decrease in downstream sediment loads, from 12 300 m³/a to 2140 m³/a. Despite the massive reductions in downstream sediment loads no bed degradation was induced by impoundment because regulated flows and dam spills are incompetent to transport the bed material. Slight but spatially disjunct channel contraction has occurred in response to flood suppression. Bank erosion rates are very low due to a combination of flood suppression, bank protection works and willow plantings. Willow invasion has been triggered by a combination of flow regulation and river management works, and is developing into a serious problem.

THE mid-Goulburn River refers to the river channel between Eildon Pondage and Lake Nagambie (Fig. 1). This section is part of the 430 km long Goulburn River corridor which was proclaimed a Heritage River by the Land Conservation Council (1991). Eildon Reservoir has regulated streamflows throughout the mid-Goulburn River since 1922 (Speedie 1948). However, the downstream effects of Eildon Reservoir on channel stability have not been assessed previously although flow regulation has often been blamed for causing river bank erosion (Hills 1975; Land Conservation Council, 1991). Furthermore, recent work on the downstream environmental impacts of Eildon Reservoir has concentrated on wetland inundation and water quality (Gippel et al. 1991; Gippel & Finlayson 1993). The purpose of this paper is to assess the downstream impacts of Eildon Dam on the flow regime, sediment load and channel stability of the mid-Goulburn River. In particular, the effects of dam-induced changes in fluvial processes on channel morphology will be determined.

Petts (1980) categorised the downstream effects of dams in terms of three orders of impacts. First-order impacts cover the downstream effects of dams on streamflows, water quality and sediment loads, and determine the magnitude of river response. Petts & Lewin (1979) found that dams often cause a decrease in both:

(i) the magnitude, frequency and duration of flood flows, and

(ii) the quantity and calibre of the sediment load.

Second-order impacts refer to the changes in channel form resulting from the first-order impacts. Channel readjustment will only occur if the process changes are of sufficient magnitude to disrupt equilibrium. The scientific literature since the early part of this century is replete with examples of downstream channel changes subsequent to dam closure (see Petts 1979; Williams & Wolman 1984). Third-order impacts include the feedback effects of the morphological changes upon the ecology or vice versa. Stable or depositional sites are good seed beds for phreatophytes which often invade channels after flow regulation (Williams & Wolman 1984; Sherrard & Erskine 1991; Benn & Erskine 1994). The three orders of impact of Eildon Reservoir on the mid-Goulburn River will be outlined after first discussing the salient characteristics of the dam. This information is necessary to form

the basis of river management strategies for the mid-Goulburn River.

EILDON RESERVOIR

Eildon Reservoir is located on the Goulburn River immediately downstream of the junction of the Goulburn and Delatite Rivers (Fig. 1) where the catchment area is 3885 km^2. The original impoundment at Eildon was known as Little Eildon or Sugarloaf Reservoir and was built between 1915 and 1927 (Knight 1948). Selected characteristics of the original dam and the resultant lake are contained in Table 1. In 1929 the rockfill on the upstream portion of the dam wall subsided over a length of 366 m when the reservoir was drawn-
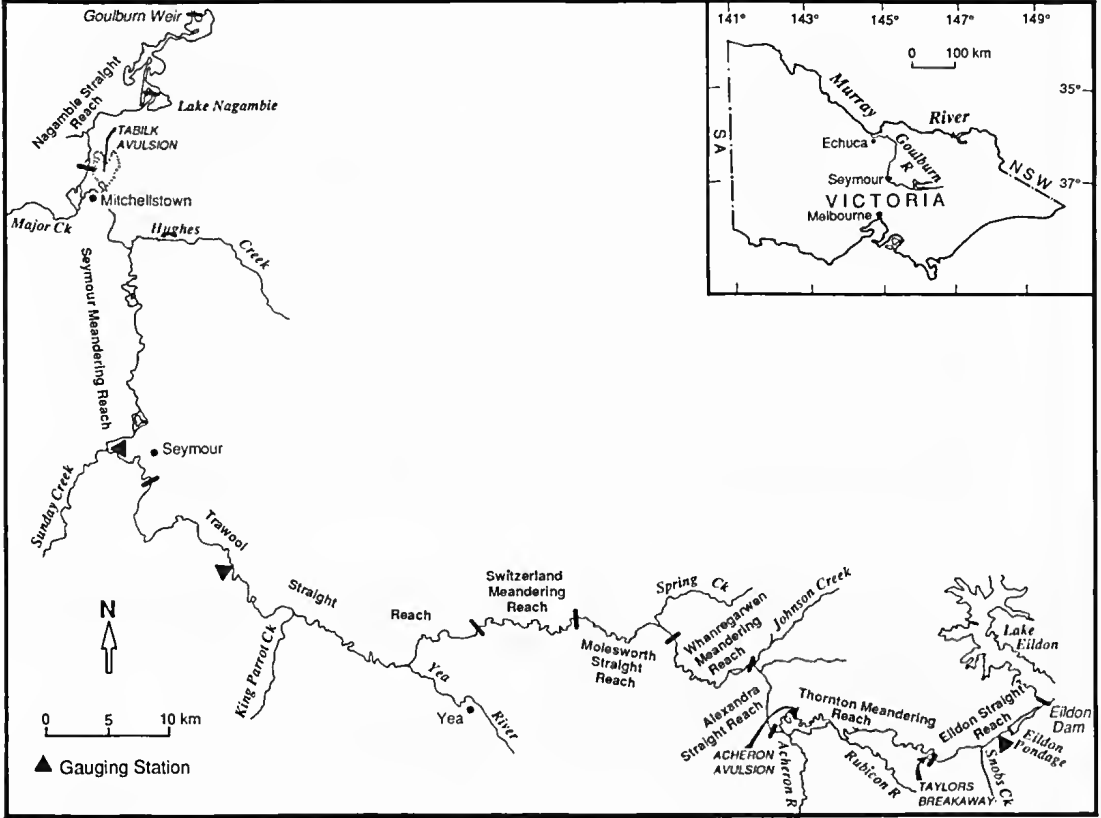
Fig. 1. Mid-Goulburn River between Eildon Reservoir and Lake Nagambie, showing alternating straight and meandering reaches.

	Original Eildon Dam, Little Eildon Reservoir	New Eildon Dam, Big Eildon Reservoir
Storage capacity at full supply level (ML)	377 450	3 390 100
Surface area (ha)	3 075	13 750
Shoreline (km)	—	466
Maximum depth (m)	37.5	76.2
Mean depth (m)	12.3	23.9
Average annual inflow (ML/a)	1 917 850[1]	1 645 000[2]

[1] From Knight (1938).   [2] From Powling (1980).

Table 1. Major physical and morphometric characteristics of Little and Big Eildon Reservoirs (from Knight 1938; Cadwallader 1980; Powling 1980; Collier 1986).

down from full supply level for the first time. (Knight 1938). This necessitated remedial measures which stabilised the dam (Knight 1938). The original dam was to be built in two stages with the second stage involving the raising of the dam wall by 16 m thus increasing the storage capacity threefold (Collier 1986). However, such enlargement was abandoned following the subsidence of the dam wall.

The purpose of the reservoir was to supply irrigation water to Lake Nagambie for distribution to the Goulburn–Murray Irrigation District. Water was released through either the main or power outlet and then conveyed down the natural channel to Lake Nagambie. Increasing demand for additional supply to the Goulburn–Murray Irrigation District resulted in the construction of the new, larger Big Eildon Reservoir immediately downstream of the original dam (Knight 1948; Speedie 1948). It was built between 1950 and 1955 and, when completed, was the largest reservoir in Australia. Selected characteristics of the new dam and the resultant lake are also contained in Table 1. Eildon Reservoir is a 'carry-over' dam which means that its storage capacity is larger than the mean annual flow. Sugarloaf Reservoir, on the other hand, had no carry-over capacity. Water can be released from the new dam at rates up to 9500 ML/d and is usually passed through two generators which have a total power output of 120 MW (Rural Water Commission undated). The original dam also had a power station but its total output was only 15 MW. The present hydro-power releases are passed into a 5200 ML pondage below the new dam so that the flows can be re-regulated to:

  (i) contain releases within the capacity of the channel,
  (ii) reduce bank erosion and slumping, and
  (iii) minimise danger to anglers and others using the river (Frost 1983).

Since 1959 Eildon Reservoir has been operated according to a set of rules known as 'Mark Operation', which include a target filling curve which aims to fill the storage by 1 October each year (State Rivers and Water Supply Commission 1981). If the reservoir is at target storage volume in May, there is a high probability of inflows between May and September being sufficient to fill the dam by 1 October (State Rivers & Water Supply Commission 1981). When inflows exceed the target, controlled releases are made at a rate dependent upon the prescribed allowable maximum flows at Seymour (these are not defined in State Rivers & Water Supply Commission, 1981). This

constraint can, in fact, lead to releases being less than inflows, resulting in target levels being exceeded.

Detailed limnological surveys of Eildon Reservoir by Powling (1971, 1972, 1980) have established that the artificial lake is oligotrophic (low nutrient levels) and warm, monomictic (summer thermal stratification with holomixis or overturn at temperatures above 4°C at other times). Lake Eildon is thermally stratified between October and May. Overturn usually occurs in July when profundal nematods and rhizopods are found in surface water samples.

Thermal stratification is important because water is removed from the hypolimnion (the cold water zone) at a depth of 52 m for the outlets. As a result, the annual range in downstream monthly median water temperature has been reduced from 7.4–19.5°C to 9.9–13.5°C, with summer temperatures depressed and winter temperatures elevated above natural values (Gippel & Finlayson 1993).

FIRST-ORDER IMPACTS

The first-order impacts of Eildon Reservoir to be outlined below include downstream hydrologic changes and reduced sediment loads.

Hydrologic changes

Little Eildon Reservoir commenced storing water in July 1922 and Big Eildon Reservoir, in June 1955. Therefore, where data exist, the hydrologic records will be split into the pre-dam period (before July 1922), the Little Eildon Reservoir period (July 1922 to May 1955) and Big Eildon Reservoir period (June 1955 to September 1991). In this section changes in annual runoff, monthly runoff, mean daily discharge and flood peak discharge will be determined.

Annual runoff. The gauging station on the Goulburn River at Eildon commenced on 1 January 1916 and has operated continuously since then. The present gauge is located 800 m downstream of the regulating weir. The Rural Water Corporation has estimated 'natural' streamflows at the Eildon gauge since July 1922 by the following equation:

$$Q_N = \delta S + Q_R + E \tag{1}$$

where Q_N is estimated natural flow at Eildon,
      δS is change in lake storage,
      Q_R is regulated flow at Eildon, and
      E is evaporation from the reservoir surface.

These estimated natural streamflows have been tabulated on a monthly basis and used in the following analyses. This data set was *not* used in the previous hydrologic work on Eildon Reservoir by Gippel et al. (1991) and Gippel & Finlayson (1993).

Between July 1922 and May 1955 when Sugarloaf Reservoir was operational, the variance of annual regulated flow was not statistically significantly ($\propto = 0.05$) different to the variance of annual estimated natural flow (F test). Although the mean annual regulated runoff was 39 614 ML less than the mean annual natural runoff, this difference is not significant ($\propto = 0.05$) according to a t-test. This reduction in runoff equates to an evaporation loss of 1288 mm/a from Little Eildon Reservoir, assuming that the dam was always at full supply level.

Between June 1955 and September 1991, the variance of annual regulated flow was significantly less than the variance of annual natural flow. As the variances of the two data sets are not equal, a t-test cannot be used to assess differences in means. Therefore, the Z-test (Crow et al. 1960) was used and showed that the reduction in mean annual runoff of 122 902 ML by flow regulation was not significantly different to the mean annual natural runoff. This reduction in runoff equates to an evaporation loss of 821 mm/a from Big Eildon Reservoir, assuming that the dam was always at full supply level. This discrepancy in the two evaporation estimates for Little and Big Eildon Reservoirs can be explained by greatly reduced summer evaporation from the deeper Big Eildon Reservoir (Garrett & Hoy 1978).

Monthly runoff. The Rural Water Corporation data set used above was also analysed for changes in the variance and mean between regulated and estimated natural flows for each month. Again the data was split into the two time periods covering the operation of Little and Big Eildon Reservoirs. The same statistical tests were used as in the above section. The results for each month and for both time periods are summarised in Table 2.

Figure 2A shows the changes in mean monthly regulated and natural flows during the operation of Little Eildon Reservoir. Clearly, regulated flows significantly exceeded natural flows between December and April, inclusive during the irrigation season (Table 2). The period May to September marked the replenishment of stored water released for the preceding irrigation season.

Figure 2B shows the changes in mean monthly regulated and natural flows during the operation of Big Eildon Reservoir. In general terms, the

Month	Sugarloaf Reservoir July 1922– May 1955		Eildon Reservoir June 1955– September 1991	
	Variance	Mean	Variance	Mean
January	*	*	*	*
February	*	*	*	*
March	N.S.	*	*	*
April	*	*	*	*
May	*	N.S.	*	*
June	N.S.	N.S.	*	*
July	N.S.	*	*	*
August	N.S.	*	*	*
September	N.S.	N.S.	N.S.	*
October	N.S.	N.S.	N.S.	*
November	N.S.	N.S.	N.S.	*
December	N.S.	*	N.S.	*

*—Significant at $\propto < 0.05\%$.
N.S.—Not significant at $\propto = 0.05\%$.

Table 2. Changes in the variance and mean between monthly regulated flow and monthly natural flow. See text for further details.

hydrologic effects of Big Eildon Reservoir on monthly flows are the same as for Little Eildon Reservoir but the magnitude and hence, significance of the changes is much greater. Furthermore, while Little Eildon Reservoir influenced the seasonal flow distribution, the natural pattern was maintained with high winter and spring flows and low summer and autumn flows. On the other hand, Big Eildon Reservoir has totally reversed the natural seasonal flow pattern with maximum flows in summer and autumn, and minimum flows in winter and spring (Gippel et al. 1991; Gippel & Finlayson 1993).

Flow durations. Flow duration curves based on mean daily discharge were prepared for the above three time periods. Fig. 3A shows the curves for each of these periods. Although the pre-dam data are used as an index of natural flow conditions, it must be stressed that the record is very short and contains two wet years (1916 and 1917). Little Eildon Reservoir truncated all flows above 82 000 ML/d, decreased the magnitude of flows with durations less than 36%, increased the magnitude of flows with durations between 36 and 87% and decreased the magnitude of flows with durations greater than 87% (Fig. 3A). The larger flows with durations between 36 and 87% (600–4000 ML/d) coincide with the irrigation releases. Big Eildon Reservoir further truncated high flows with no discharges greater than 46 200 ML/d having been recorded between
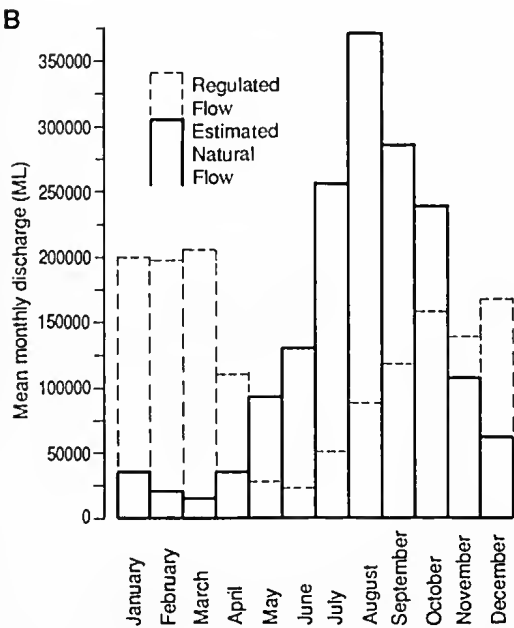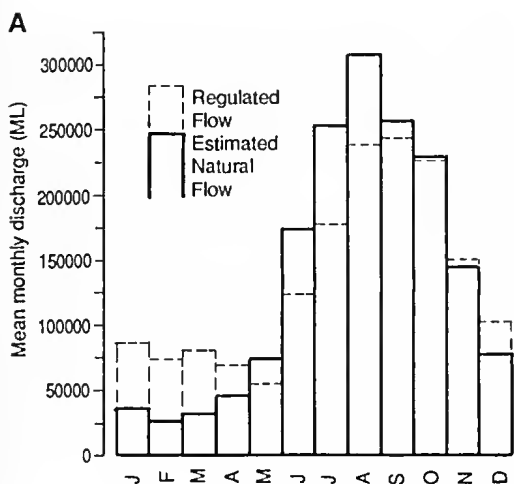
Fig. 2. A, Changes in mean monthly regulated flow and mean monthly natural flow at the Eildon gauging station between July 1922 and May 1955. B, Changes in mean monthly regulated flow and mean monthly natural flow at the Eildon gauging station between June 1955 and September 1991.
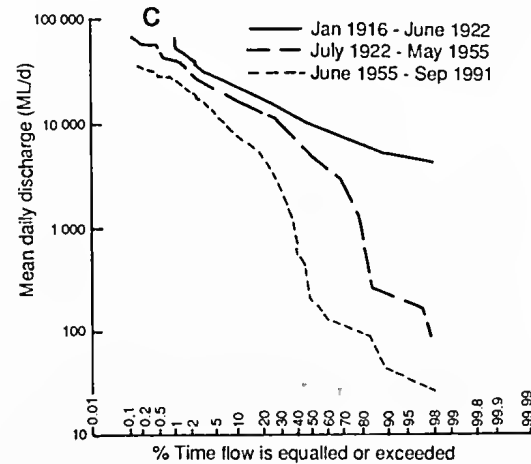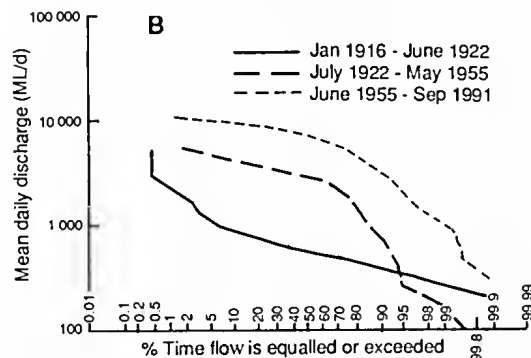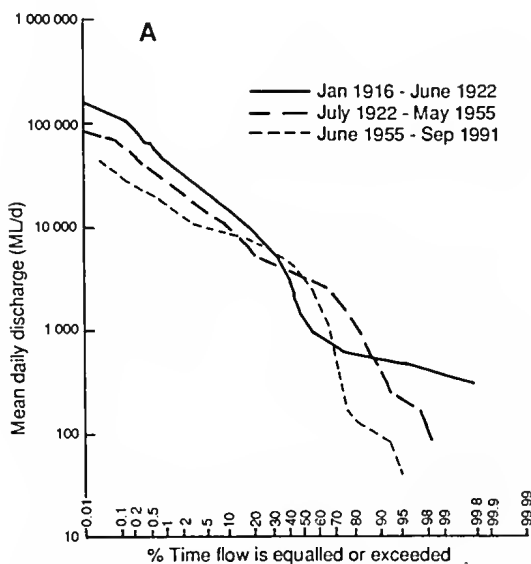
Fig. 3. A, Flow duration curves based on mean daily discharge at the Eildon gauging station for the periods January 1916 to June 1922 (natural conditions), July 1922 to May 1955 (Sugarloaf Reservoir) and June 1955 to September 1991 (Eildon Reservoir). B, Flow duration curves based on mean daily discharge for March at the Eildon gauging station. C, Flow duration curves based on mean daily discharge for August at the Eildon gauging station.

1955 and 1991. In comparison with the natural flow duration curve, Big Eildon decreased the magnitude of flows with durations less than 29%, increased the magnitude of flows with durations between 29 and 69% and decreased the magnitude of flows with durations greater than 69%. In comparison with the Little Eildon flow duration curve, Big Eildon further decreased the high flows (>8200 ML/d), augmented the moderate flows (3500–8200 ML/d) and further decreased the low flows.

To assess changes in the seasonal flow distribution caused by Little and Big Eildon Reservoirs, flow duration curves based on mean daily discharge were prepared for each month. The results are very consistent and are illustrated in Figs 3B and 3C. During the irrigation season, flow regulation has resulted in the wholesale *upward* displacement of the flow duration curve as shown for March in Fig. 3B. Under existing conditions, mean daily flow of a given duration is about an order of magnitude *greater* than under natural conditions.

Flow regulation has resulted in the storage of high winter flows and the consequent wholesale *downward* displacement of the flow duration curve as shown for August in Fig. 3C. The curves for Little and Big Eildon Reservoirs increasingly diverge from the curve for natural conditions for durations greater than about 20%. The maximum decrease in discharge for a given duration is greater than two orders of magnitude.

Flood frequency. An automatic water level recorder was first installed at the Eildon gauge in June 1953. Before then, the gauge was daily read. As a result, peak instantaneous discharges are only available at this site since 1954. Therefore, the following flood frequency analyses at Eildon were undertaken using maximum mean daily flow.

Figure 4A shows the annual series flood frequency curves for the periods 1922–54 (Little Eildon Reservoir) and 1955–86 (Big Eildon Reservoir). The method of Dalrymple (1960) was used with the modification that plotting positions were calculated by the Gringorten (1963) equation because it is an unbiased formula for the adopted Extreme Value I distribution (Cunnane 1978; Bell et al. 1989). This method was used in preference to the log Pearson Type III distribution adopted by State Rivers & Water Supply Commission (1981) and Gippel et al. (1991) so that the results could be directly compared with the published geomorphic literature. Clearly, the enlargement of the original dam has reduced greatly flood magnitudes for a given frequency. The percentage decrease in flood magnitude for various return periods since

1955 range between 60 and 72%. A return period of 1.58 years for an Extreme Value I distribution corresponds to the mode of the distribution and a return period of 2.33 years corresponds to the mean (Gumbel 1958). It has been argued that floods of this frequency correspond to the 'dominant' or 'channel-forming discharge' (Wolman & Leopold 1957; Wolman & Miller 1960; Leopold et al. 1964; Dury 1973). Reductions in maximum mean daily flow of 65–72% for floods of these return periods closely agree with the previous results of State Rivers & Water Supply Commission (1981) and Gippel et al. (1991). It should also be emphasised that the flood frequency curve for natural floods would plot above the curve for 1922–54. However, the pre-dam record is too short to undertake flood frequency analysis.
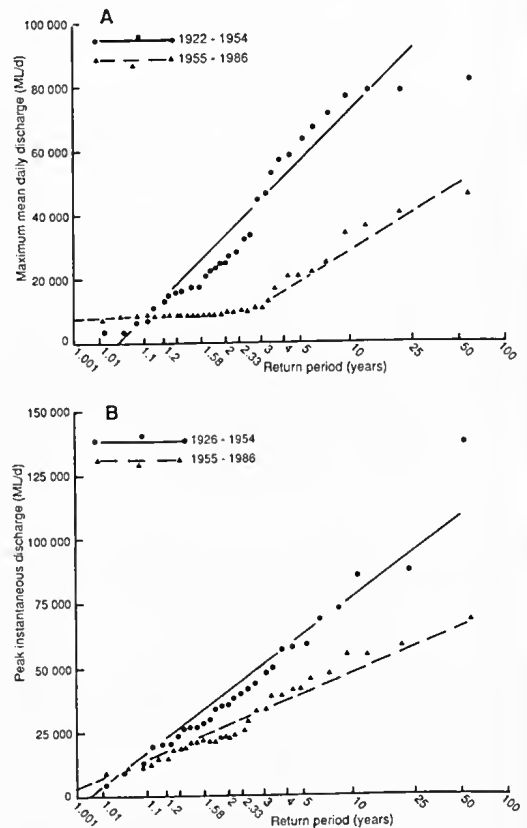
Fig. 4. A, Annual series flood frequency curves for the periods 1922–54 (Sugarloaf Reservoir) and 1955–86 (Eildon Reservoir) at the Eildon gauging station. B, Annual series flood frequency curves for the period 1926–54 (Sugarloaf Reservoir) and 1955–86 (Eildon Reservoir) at the Trawool gauging station.

Changes in flood frequency were also investigated at the downstream gauging station, Goulburn River at Trawool (Fig. 1), where the catchment area is 7335 km². A continuous record has been obtained since November 1925. However, some flood peaks were not recorded although the maximum mean daily discharge was. Therefore, the missing annual floods were estimated by regressing peak instantaneous discharge (Y) against maximum mean daily discharge (X) and the following equation was obtained:

$$Y = 250.97 + 1.037X \qquad (2)$$
$$r = 0.998 \qquad \propto < 0.001$$
$$n = 50$$

Figure 4B shows the flood frequency curves for the periods 1926–54 and 1955–86 at Trawool and clearly demonstrates that Big Eildon Reservoir has also decreased flood peak discharge for all return periods although the catchment area is 1.89 times that at Eildon. Flood runoff from the unregulated tributaries between Eildon and Trawool has reduced the effect of Big Eildon, with reductions in flood peak discharge for various return periods ranging between 32 and 38%. Although Gippel et al. (1991) reported results for this station, they did *not* use peak instantaneous discharge for their analyses.

State Rivers & Water Supply Commission (1981) undertook a detailed flood study at Seymour (Fig. 1), where the catchment area is 8601 km² (2.21 times the catchment area at Eildon Reservoir). For return periods between 2 and 100 years, peak flows were reduced by 20% which represents a lowering of flood levels of about 0.3 m. Therefore, Big Eildon Reservoir is likely to have reduced flood peak discharges throughout the mid-Goulburn River.

Changes in downstream sediment loads. Sediment trap efficiency refers to the proportion of the incoming sediment load deposited in a reservoir. Some fine-grained sediment is usually transported through a storage and passed out of the valves or over the spillway. However, all of the incoming sand and gravel are trapped in large dams. The sediment trap efficiencies of Little and Big Eildon Reservoirs have been estimated by the methods of Brune (1953). These methods were chosen because Erskine (1985) found 'a close correspondence' between the trap efficiencies estimated by Brune's (1953) design procedures and that calculated by a before and after dam comparison of measured suspended sediment loads for Glenbawn Dam, NSW. Little Eildon Reservoir had a trap efficiency of 93.0–95.3% depending on whether the capacity–watershed or capacity–inflow ratio was used. Big Eildon Reservoir has a trap efficiency of 98.5–99.5%. Clearly, both Little and Big Eildon Reservoirs have trapped most of the incoming sediment.

The reduction in downstream sediment loads can be quantified from the measured rates of dam sedimentation (Joseph 1953a, 1953b, 1960; Abrahams 1972) and from the estimated sediment trap efficiencies. Joseph (1953a, 1953b, 1960) found that the measured mean sedimentation rate in Little Eildon Reservoir was 50.8 m³/km²/yr between 1927 and 1953. Therefore, if it is assumed that the sediment trap efficiency of Little Eildon Reservoir was 94.15% (mean of the estimates determined by the capacity–watershed and capacity–inflow ratio methods), the total sediment yield was 53.96 m³/km²/a or 210 000 m³/a. As 94.15% was trapped in Little Eildon Reservoir, the mean annual sediment yield at the Eildon gauge between 1927 and 1953 was only 12 300 m³/a. Abrahams (1972) found that the mean annual sedimentation rate in Big Eildon Reservoir in 1969 was 54.51 m³/km²/a. If the sediment trap efficiency is 99% (mean of the estimates determined by the capacity–watershed and capacity–inflow ratio methods), the total sediment yield was 55.06 m³/km²/a or 214 000 m³/a which agrees closely with the sediment yield estimate for Little Eildon Reservoir. As 99% was trapped in Big Eildon Reservoir, the mean annual sediment yield at the Eildon gauge was only 2140 m³/a. Therefore, before Little Eildon Reservoir was constructed, the Goulburn River at Eildon transported about 210 000 m³/a of sediment. Little Eildon Reservoir reduced this sediment load to 12 300 m³/a and Big Eildon Reservoir further reduced it to only 2140 m³/a.

SECOND-ORDER IMPACTS

Second-order impacts refer to dam-induced channel changes. The hydrologic changes, particularly the reduced flood peak discharges, combined with the markedly reduced sediment loads are of such a magnitude that the pre-dam channel equilibrium may have been disrupted and consequently channel changes may have been initiated. Rivers respond to flow regulation in a complex manner (Petts 1979; Williams & Wolman 1984; Erskine 1985; Sherrard & Erskine 1991). Nevertheless, bed degradation or progressive bed erosion over time has been reported below many dams (Lane 1934; Petts 1979; Galay 1983). Furthermore, channel contraction by the formation of benches or berms within the pre-dam channel often occurs because of reduced down-

stream flood flows (Gregory & Park 1974; Sherrard & Erskine 1991; Benn & Erskine 1994). Channel pattern refers to river morphology as seen from the air or channel planform. As discharge and sediment load are known to be important controls on channel pattern (for example, Leopold & Wolman 1957), it would be expected that channel pattern will change when discharge and sediment load are altered drastically by flow regulation. In the remainder of this section, the impacts of Little and Big Eildon Reservoirs on bed degradation, bed mobility, channel contraction and river pattern changes on the mid-Goulburn River will be assessed.

Bed degradation

Degradation below dams has been known for some time. Lane (1935: 836), in the first of a series of papers on the topic in *Engineering News Record*, explained it thus:

'When a dam is constructed in a stream with a bed of movable material, part of the material which the stream transports will be deposited in the backwater area of the reservoir. The flow passing the dam, having been partly relieved of its load, will pick up material from the river bed below the dam and thus cause a retrogression of the bed level there.'

This can be explained by reference to the sediment transport continuity equation:

$$O_S = \delta S + I_S \qquad (3)$$

where O_S is the sediment output from a reach of river,
   I_S is the sediment input to the same reach of river, and
   δS is the change in sediment storage within the reach.

For a channel to be stable, its dimensions should vary within a narrow range about a well-defined mean condition. When this is the case, O_S will equal I_S and δS will vary within small limits. Degradation depends only on the bedload component of the total sediment load. When a large dam is built, the bedload input to the downstream channel is reduced to zero, once any construction-mobilised sediment has been removed. Therefore, if there is any bedload transport out of the downstream reach of channel, it must be entrained from either the bed or banks of the channel. Bed entrainment causes degradation. Degradation starts at the outlet works/spillway and progresses downstream over time (Galay 1983). Rates of degradation > 0.15 m/a have been reported (Lane

1934; Petts 1979). For degradation to occur, regulated flows must be capable of entraining the bed material. When flow regulation results in reduced downstream flood flows, as in the case of Little and Big Eildon Reservoirs, degradation may not occur.

The Rural Water Corporation has not monitored the response of the Goulburn River to upstream impoundment. Therefore, the rating curves for the three gauging stations on the mid-Goulburn River have been analysed to indirectly determine whether bed degradation has occurred. Specific gauge plots show variations in gauge height over time for the same discharge (Blench 1969). All data have been converted to the same gauge zero for the whole period of record at each station and all stations have natural gauge controls. Fig. 5 shows the specific gauge plots for discharges of 1000 and 10 000 ML/d at Eildon and 2000 and 10 000 ML/d at Trawool and Seymour. These discharges were chosen to cover the range of regulated flows. The Eildon plot (Fig. 5A) only covers the period since 1953 when the present gauge site was used. Clearly, there have been only minor changes in gauge height for the same discharge over this time, indicating that the channel has been very stable during the period that Big Eildon Reservoir has been operational. Rating curves are also available for the other two gauging sites at Eildon since April 1933. *No change* in the rating curves at both sites were found. Therefore, if the Goulburn River at Eildon has degraded in response to impoundment it must have occurred before 1933. This is unlikely because the channel is cut into bedrock (Thomas 1947).

The specific gauge plot at Trawool (Fig. 5B) also shows that the Goulburn River there has been remarkably stable since 1926. At Seymour (Fig. 5C), the location of the gauge was changed in 1968 and there have been more rating changes. Nevertheless, the data still do not exhibit a *definite* trend and contrast greatly to the specific gauge plots in Erskine et al. (1990) for selected unstable rivers in the Gippsland Lakes catchment. It would, therefore, appear that the mid-Goulburn River has been stable despite substantial flow regulation.

Bed mobility

Erskine (1985) found that channels are stable following upstream impoundment when regulated flows do not exceed the threshold of motion of the bed material. To determine if this is the case on the mid-Goulburn River, the competence of regulated flows was determined at each gauging station. The particle size characteristics of the bed

material were determined by carrying out gravel counts according to the grid-by-number technique of Wolman (1954) at each gauge. The b-axis diameter of at least 100 gravel clasts was measured on submerged side bars and riffles at each site. The competence of maximum regulated flows (assumed to be 10 000 ML/d) was determined by the Meyer-Peter and Müller (1948) criterion at each gauging station. Effective diameter of the bed material was equated to mean size. Regulated and bank-full flows are *not* competent to mobilise the bed material at all stations. Therefore, the lack of degradation on the mid-Goulburn River since dam closure is explained by the very infrequent occurrence of threshold of motion conditions for bed material transport.

The only sections of the mid-Goulburn River which have degraded in recent years are located near gravel extraction sites at Seymour and Alexandra. Degradation at these sites has been caused by extraction creating local sediment transport discontinuities (Erskine 1990).
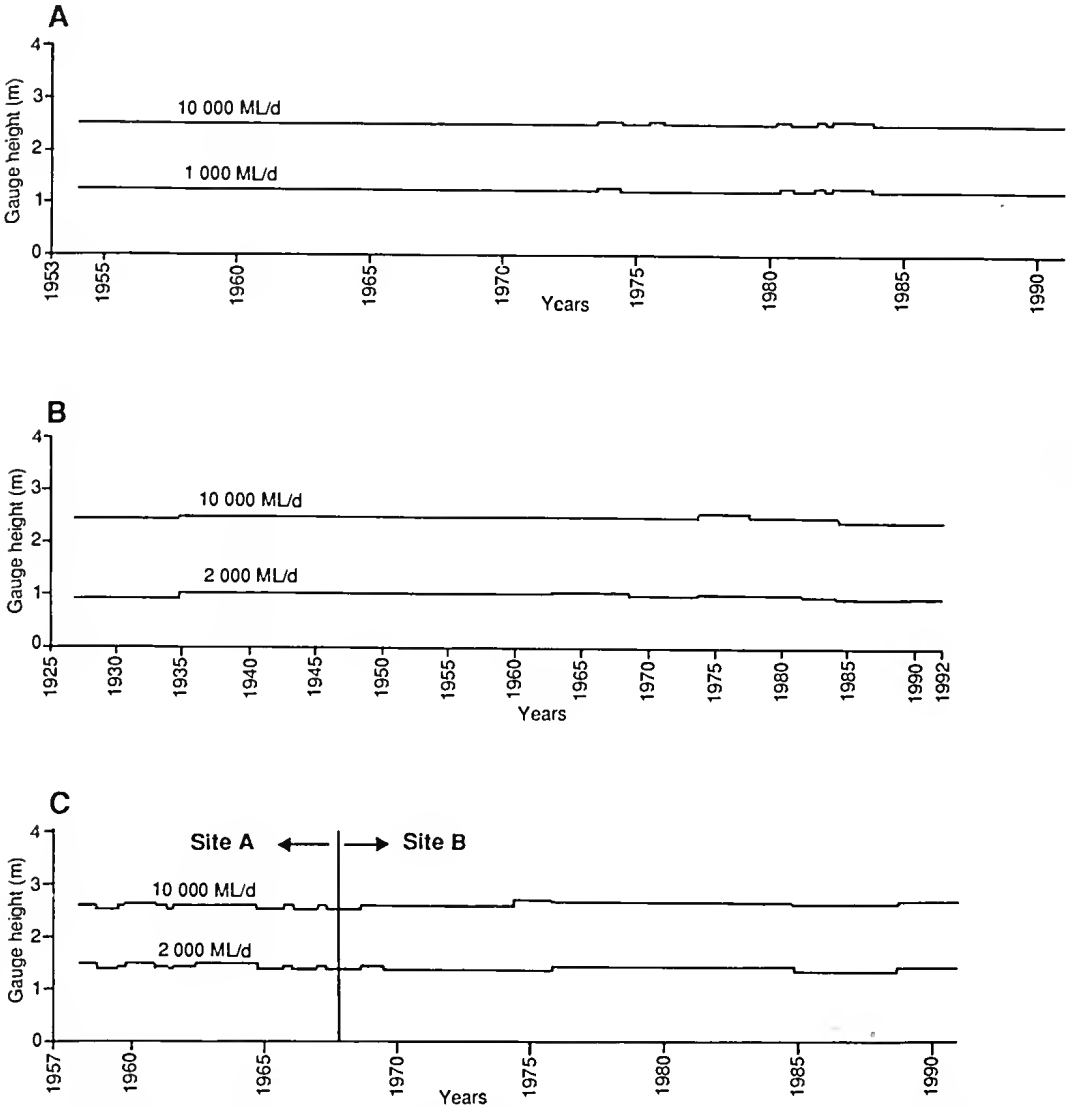
Fig. 5. Specific gauge plots. A, Eildon gauging station. B, Trawool gauging station. C, Seymour gauging station.

An armour layer is a surficial, thin, often monolayer of coarse bed material overlying finer sediment (Erskine et al. 1985; Erskine 1985, 1992). It is generally both coarser and better sorted than the subsurface sediment (Gomez 1984; Erskine 1992). The armour layer veneers the bed surface and hence protects the underlying finer sediment from erosion. Irrigation flows during the field work phase of this study prevented a detailed sedimentological study of the bed material in the mid-Goulburn River. Nevertheless, it appears from field inspections that the bed is armoured. If this is the case, the natural armour coat must be retained intact to prevent localised degradation.

Channel contraction

Channel width is adjusted to dominant discharge according to a simple power function. Kellerhals (1967) found that, on armoured gravel-bed streams, bankfull width is related to dominant discharge by the following equation:

$$W = 0.635Q^{0.5} \qquad (4)$$

where   W is channel width, (m), and
Q is dominant discharge (m^3/s).
Therefore, if dominant discharge decreases due to flow regulation, as has occurred on the mid-Goulburn River, channel width should decrease, provided there is a source of sediment for deposition within the overwide pre-dam channel. From the above equation, it is predicted that the channel will contract by up to 59 m because the mean annual flood has been reduced by up to 72%. Although there are no permanently marked, long term cross sections on the mid-Goulburn River to test this prediction, the following indirect evidence suggests that recent discontinuous channel contraction has occurred:

   (i) the river banks are well vegetated and stable;
   (ii) low berms, benches and bars of sand, gravel and mud are discontinuously present along the side of the channel below the river bank in many locations;
   (iii) trees growing on these berms, benches and bars are relatively young as shown by their small diameters and low heights; and
   (iv) soils developed on these landforms correspond to the stratic stage alluvial soils of Walker & Coventry (1976) which are known to be relatively young (<200 years).

The berms, benches and bars are preferentially located near local sediment sources, such as unregulated tributary junctions, cutoffs or formerly eroding banks. A similar situation has been documented on the Cudgegong River below Windamere Dam in New South Wales (Benn & Erskine 1994). However, these in-channel benches on the mid-Goulburn River are spatially disjunct and very narrow because of the limited sediment supply.

River pattern changes

There have been two types of channel pattern changes on the mid-Goulburn River, viz lateral migration/bank erosion and channel avulsions. Each of these will now be discussed in turn.

Lateral migration. The Master Plans prepared for the three former River Improvement Trusts which carried out river management works on the mid-Goulburn River, all refer to bank erosion as a problem and as one of the reasons leading to the formation of the Trusts (Ian Drummond & Associates 1984a, 1984b; Willing & Partners 1984). While snags, gravel bars and regulated flows were mentioned as significant causes of bank erosion, lateral migration and meander development were also recognised as being significant.

The mid-Goulburn River exhibits alternating reaches of straight and meandering channels (Thomas 1947; Erskine et al. 1993). Fig. I shows the location of these reaches. It must be stressed that, while it is relatively easy to identify these alternating straight and sinuous sections, the boundary between them is far from clear cut. Therefore, the boundaries shown in Fig. 1 should be viewed as being approximate only. The channel patterns adopted in Fig. I are taken from Leopold & Wolman (1957) who recognised straight, meandering and braided channels. Straight channels had a sinuosity (ratio of channel length to valley length and used as an index of the degree of meandering) of less than 1.5 and meandering channels, greater than or equal to 1.5. The reasons for these alternating straight and meandering sections are unclear. Measurements of valley slope from the State Rivers & Water Supply Commission's 1935 Goulburn River Survey Plans (30023 to 30028) for the various reaches showed little, if any difference between straight and sinuous sections. Therefore, valley slope does not explain the channel pattern changes in contrast to the situation on the Mississippi River reported by Schumm et al. (1972). Although valley width is less on most straight reaches than on most meandering reaches, this is not always the case. If the straight reaches were formerly meandering and have straightened by cutoffs then the rate of meander development must be very slow.

Comparison of the first surveys of the mid-Goulburn River (Pickering 1841; Pinninger 1856; Anon. 1860) and the State Rivers and Water Supply Commission's 1935 surveys with present channel conditions shows a few cutoffs and avulsions but relatively minor lateral migration. In fact, the bank erosion rates on the mid-Goulburn River are less than Hooke's (1980) minimum rates measured on rivers of comparable size throughout the world.

The density of riparian trees, particularly willows has increased greatly as a result of plantings by the former River Improvement Trusts and by the present North Central Waterways Management Board. Willows and, in some cases, River Red Gums, have formed extensive root mats. Smith (1976) has demonstrated that thick root mats can increase sediment resistance by 10 000 times over a bare bank. Flow regulation, by decreasing peak discharges and hence stream power, and river management works, by planting trees on the banks and by placing rockfill and other structural works, have increased bank resistance. Therefore, lateral migration and bank erosion rates are now very slow on most of the mid-Goulburn River.

Channel avulsions. Channel avulsions are the wholesale abandonment of one river course for another at a lower level on the floodplain (Allen 1965). There has been one recent avulsion on the mid-Goulburn River at Acheron (Thompson 1938), and another was occurring at Taylors Breakaway near Thornton (Turnbull 1957), before engineering works were undertaken to stop the river diversion. The Acheron avulsion probably occurred in July 1931 by the second largest flood to be passed through Little Eildon Reservoir (Erskine et al. 1993) and will not be discussed further.

Taylor's Breakaway is a crevasse, gulch or breach of the natural levee of the Goulburn River at the apex of a cutoff about 11 km downstream of Eildon Reservoir at the start of the Thornton meandering reach (Fig. 6). This cutoff occurred between the surveys of Pinninger (1856) and State Rivers & Water Supply Commission (in 1935). Nevertheless, overbank flow still passed through Taylors Breakaway after the cutoff had been effected. The overbank flow split and either flowed down a series of floodplain depressions into the Rubicon River or through another series of depressions to Thornton (Fig. 6). The initial maximum releases from Eildon Reservoir caused substantial scour of the crevasse. To prevent an avulsion from occurring due to prolonged regulated flows, the State Rivers & Water Supply Com-
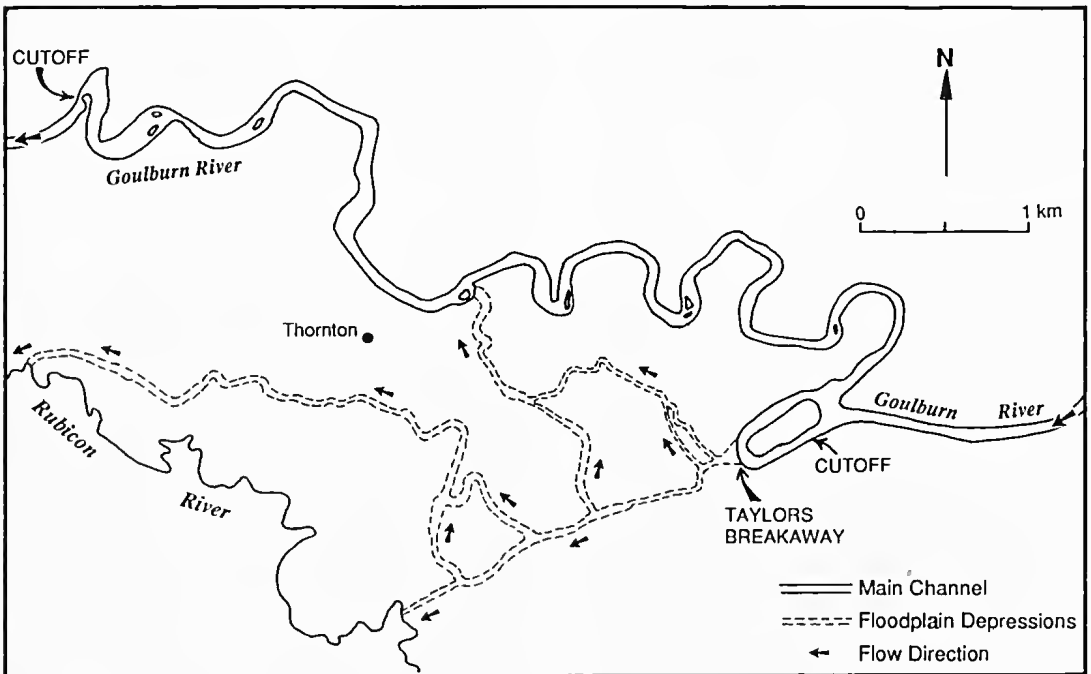
Fig. 6. Potential avulsion at Taylor's Breakaway. See Fig. 1 for location.

mission built a sheet pile weir at the crevasse. Turnbull (1957) discusses this structure in detail. Recent field inspections revealed that the sheet pile weir has successfully prevented a major avulsion from occurring. In this case, regulated flows would have caused an avulsion if appropriate engineering works had not been undertaken.

THIRD-ORDER IMPACTS

Third-order impacts reflect the feedback effects of the morphological changes upon the ecology or vice versa, and occur with a considerable time-lag in relation to the first-order changes of processes (Petts 1980). The most important third-order impact from a geomorphic perspective is vegetation encroachment on the regulated main stream. Although there are many other third-order impacts, these are solely of an ecological nature and are discussed elsewhere (see Walker et al. 1978; Baxter 1977; Walker 1985; Gippel & Finlayson 1993 for further details).

Vegetation encroachment

Regulated rivers are often invaded by vegetation because they have a stable substrate and because there is an absence of large disruptive floods. Furthermore exposed bars and benches with shallow water tables are good sites for phreatophytes. On the mid-Goulburn River, *Salix* spp., *Eucalyptus* spp. and *Acacia* spp. are common along many sections of channel. *Salix* spp. is a major problem on many regulated streams in Australia (Erskine 1985). Comparison of today's conditions with those depicted in old photographs taken by the various River Improvement Trusts clearly demonstrates that willows have invaded long sections of river. River Improvement Trusts planted willows for bank erosion control (Erskine et al. 1993) and many of the willow stands represent these extended plantings. The regulated flow conditions during the operation of Eildon Reservoir exhibit smaller flood peak discharges and reduced flood variability (Figs 4A and 4B). Therefore, the survival of large numbers of planted willows should have been predicted. While willows undoubtedly stabilise formerly eroding banks, they can rapidly develop into a problem. They can increase roughness significantly, accelerate deposition and reduce species diversity. Now that there are extensive but spatially disjunct stands of willows on a highly regulated stream they will invade the intervening areas to form a continuously willow-lined channel. The rate of invasion seems to be relatively slow with thick stands taking about

30 years to develop. Extensive willow control is necessary to avoid the loss of native species from the riparian corridor.

DISCUSSION AND CONCLUSIONS

The construction and operation of Little and Big Eildon Reservoirs has resulted in significant downstream hydrologic changes on the mid-Goulburn River. Gippel and Finlayson (1993) concluded that these hydrologic changes in combination with lowered spring and summer water temperatures alienated the Goulburn River between Eildon and Seymour from habitation by native fish species. While similar explanations of the demise of native fish on inland regulated rivers have been published (Cadwallader 1978), recent research has demonstrated that the iridovirus, epizootic haematopoietic necrosis (EHN), has also played a major role in the population decline of at least *Macquaria australasica, Galaxias olidus* and *Bidyanus bidyanus* (Langdon 1989). EHN is the first virus to be found in Australian fish (Langdon 1986) and the disease is characterised by necrosis of the renal haematopoietic tissue, liver, spleen and pancreas (Langdon & Humphrey 1987). While EHN is extremely infectious and pathogenic for the introduced *Perca fluviatilis*, some native species are also highly susceptible to in-water transmission and others are potential carriers and host species (Langdon 1989). EHN has been found in Lake Eildon and the Goulburn River downstream (Langdon & Humphrey 1987). Therefore, the well documented demise of native fish species in the mid-Goulburn River has most probably been caused by the interaction of hydrologic and water quality changes with the infectious and often pathogenic iridovirus EHN plus the introduction of exotic fish species (Cadwallader 1986).

Flow regulation has significant implications for river management. The substantial reduction in flood discharges has greatly reduced the extent and rate of bank erosion. Bank stabilisation works are not a contemporary priority issue on most of the mid-Goulburn River. Reduced bank erosion and the high sediment trap efficiency of Big Eildon Reservoir has reduced downstream sediment supply and flood suppression has reduced the frequency of, if not totally stopped, bed load transport on the mid-Goulburn River. Extractive industries are, therefore, removing a non-sustainable resource, inducing local bed erosion in the process (Erskine 1990). They should now be managed so that extraction is only allowed where it achieves river management objectives. Furthermore, if the bed of the mid-Goulburn River is armoured, then

extraetion will destabilise this protective eoating. Further investigations of bed stability are clearly required.

Willow invasion of the riparian corridor is a major problem whieh has been partly induced by flow regulation. A riparian vegetation management plan is needed for the mid-Goulburn River to address the problems of inereased resistanee to flow, ehannel bloekages, redueed speeies diversity, willow replaeement, regeneration of native species, bank stability and habitat maintenanee.

River management of the mid-Goulburn River should be earried out by a single authority with jurisdietion for the whole reaeh between Eildon Pondage and Lake Nagambie. River management issues, strategies and plans are similar for the whole reaeh and should be implemented by this single body.

ACKNOWLEDGEMENTS

REFERENCES

ABRAHAMS, A. D., 1972. Drainage densities and sediment yields in eastern Australia. *Australian Geographical Studies* 10: 19–41.

ALLEN, J. R. L., 1965. A review of the origin and characteristics of recent alluvial sediments. *Sedimentology* 5: 89–191.

ANONYMOUS, 1860. *Plan of upper Goulburn River*. Central Plan Office Plan No. Goulburn 6A.

BAXTER, R. M., 1977. Environmental effects of dams and impoundments. *Annual Review of Ecology and Systematics* 8: 255–283.

BELL, F. C., DOLMAN, G. S. & KHU, J. F., 1989. Frequency estimation of natural hazards and extremes. *Australian Geographical Studies* 27: 67–86.

BENN, P. C. & ERSKINE, W. D., 1994. Complex channel response to flow regulation: Cudgegong River below Windamere Dam, Australia. *Applied Geography* 14: 153–168.

BLENCH, T., 1969. *Mobile Bed Fluviology: a Regime Theory Treatment of Canals and Rivers for Engineers and Hydrologists*. University of Alberta Press, Edmonton.

BRUNE, G. M., 1953. Trap efficiency of reservoirs. *Transactions of the American Geophysical Union* 34: 407–418.

CADWALLADER, P. L., 1978. Some causes of the decline in range and abundance of native fish in the Murray–Darling River system. *Proceedings of the Royal Society of Victoria* 90: 211–224.

CADWALLADER, P. L., 1983. A review of fish stocking in the larger reservoirs of Australia and New Zealand. *F.A.O. Fish Circular, (757)*.

CADWALLADER, P. L., 1986. Fish of the Eildon District. In *Eildon: The Whole Dam Story*. Eildon Primary School, Eildon, 40–49.

COLLIER, K., 1986. Sugarloaf Dam. In *Eildon: The Whole Dam Story*. Eildon Primary School, Eildon, 11–15.

CROW, E. L., DAVIS, F. A. & MAXFIELD, M. W., 1960. *Statistics Manual*. Dover Publications, New York.

CUNNANE, C., 1978. Unbiased plotting positions—a review. *Journal of Hydrology* 37: 205–222.

DALRYMPLE, R., 1960. Flood frequency analyses. *U.S. Geological Survey Water Supply Paper 1543-A*.

IAN DRUMMOND & ASSOCIATES PTY LTD, 1984a. *Master Plan*. Seymour Shire River Improvement Trust, Seymour.

IAN DRUMMOND & ASSOCIATES PTY LTD, 1984b. *Master Plan*. Shire of Alexandra River Improvement Trust, Alexandra.

DURY, G. H., 1973. Magnitude-frequency analysis and channel morphometry. In *Fluvial Geomorphology*. M. Morisawa, ed., George Allen and Unwin, London, 91–121.

ERSKINE, W. D., 1985. Downstream geomorphic impacts of large dams: the case of Glenbawn Dam, NSW. *Applied Geography* 5: 195–210.

ERSKINE, W. D., 1990. Environmental impacts of sand and gravel extraction on river systems. In *The Brisbane River: A Source Book for the Future*. P. Davie, E. Stock & D. Low Choy, eds, Australian Littoral Society Inc. and Queensland Museum, Brisbane, 295–302.

ERSKINE, W. D., 1992. Channel responce to large-scale river training works: Hunter River, Australia. *Regulated Rivers: Research and Management*, 7: 261–278.

ERSKINE, W. D., GEARY, P. M. & OUTHET, D. N., 1985. Potential impacts of sand and gravel extraction on the Hunter River, New South Wales. *Australian Geographical Studies* 23: 71–86.

ERSKINE, W. D., RUTHERFURD, I. D., LADSON, A. R. & TILLEARD, J. W., 1993. *Fluvial Geomorphology of the Goulburn River Basin*. Mid-Goulburn Catchment Co-ordinating Group Inc.

ERSKINE, W. D., RUTHERFURD, I. D. & TILLEARD, J. W., 1990. *Fluvial Geomorphology of Tributaries to the Gippsland Lakes*. Dept of Conservation and Environment Vic., Melbourne.

FROST, A. C. H., 1983. *Hydro-Electricity in Australia*. Australian Government Publishing Service, Canberra.

GALAY, V. J., 1983. Causes of river bed degradation. *Water Resources Research* 19: 1057-1090.

GARRETT, D. R. & HOY, R. D., 1978. A study of monthly lake to pan coefficients using a numerical lake model. *Hydrology Symposium, Canberra 5-7 Sept. 1978, Institution of Engineers Australia,* 145-149.

GIPPEL, C. J. & FINLAYSON, B. L., 1993. Downstream environmental impacts of regulation on the Goulburn River, Victoria. *Hydrology and Water Resources Symposium, Newcastle 30 June-2 July 1993, Institution of Engineers Australia,* 33-38.

GIPPEL, C. J., FINLAYSON, B. L. & THOMPSON, B. A., 1991. Establishing the effect of river regulation on wetland flooding regimes. In *Rapid Techniques for Assessing Wetland Vegetation and Water Regime, Part II.* Bureau of Rural Resources, Dept of Primary Industries and Energy, Canberra Working Paper No. WP/12/91 86-129.

GOMEZ, B., 1984. Typology of segregated (armoured/paved) surfaces: some comments. *Earth Surface Processes and Landforms* 9: 19-24.

GREGORY, K. J. & PARK, C. C., 1974. Adjustments of river channel capacity downstream from a reservoir. *Water Resources Research* 10: 870-873.

GUMBEL, E. J., 1958. Statistical theory of floods and droughts. *Journal of the Institution of Water Engineers* 12: 157-184.

GRINGORTEN, I. I., 1963. A plotting rule for extreme probability paper. *Journal of Geophysical Research* 68: 813-814.

HILLS, E. S., 1975. *Physiography of Victoria: An Introduction to Geomorphology.* Whitcombe and Tombs, Melbourne.

JOSEPH, O. F. F., 1953a. Siltation of reservoirs. Eildon surveys analysed. *Aqua* 5 (November): 19-23.

JOSEPH, O. F. F., 1953b. *Report on Siltation of Eildon Reservoir.* State Rivers and Water Supply Commission, Melbourne.

JOSEPH, O. F. F., 1960. Siltation of reservoirs. Recent surveys. *Aqua* 12 (November): 67-69.

KELLERHALS, R., 1967. Stable channels with gravel-paved beds. *Journal of the Waterways and Harbours Division American Society of Civil Engineers* 93: 63-84.

KNIGHT, R. G., 1938. The subsidence of a rockfill dam and the remedial measures employed at Eildon Reservoir, Australia. *Journal of Institution of Civil Engineers* 5: 111-191.

KNIGHT, R. G., 1948. Eildon Reservoir enlargement project, Victoria. *Journal of the Institution of Engineers Australia* 20: 73-80.

LAND CONSERVATION COUNCIL, 1991. *Rivers and Streams Special Investigation Final Recommendations.* Victorian Government Printer, Melbourne.

LANE, E. W., 1934. Retrogression of levels in riverbeds below dams. *Engineering News Record* 1934: 836-838.

LANGDON, J., 1986. A new viral disease of redfin perch. *Australian Fisheries* 38: 35-36.

LANGDON, J., 1989. Experimental transmission and pathogenicity of epizootic haematopoietic necrosis virus (EHNV) in redfin perch, *Perca fluviatilis* L., and 11 other teleosts. *Journal of Fish Diseases* 12: 295-310.

LANGDON, J. S. & HUMPHREY, J. D., 1987. Epizootic haematopoietic necrosis, a new viral disease in redfin perch, *Perca fluviatilis* L., in Australia. *Journal of Fish Diseases* 10: 289-297.

LEOPOLD, L. B. & WOLMAN, M. G., 1957. River channel patterns: braided, meandering and straight. *U.S. Geological Survey Professional Paper 282-B.*

LEOPOLD, L. B., WOLMAN, M. G. & MILLER, J. P., 1964. *Fluvial Processes in Geomorphology.* Freeman and Co., San Francisco.

MEYER-PETER, E. & MÜLLER, R., 1948. Formulas for bedload transport. *Proceedings second Meeting International Association of Hydraulic Structures Research, Stockholm* 39-64.

PETTS, G. E., 1979. Complex response of river channel morphology subsequent to reservoir construction. *Progress in Physical Geography* 3: 329-362.

PETTS, G. E., 1980. Long-term consequences of upstream impoundment. *Environmental Conservation* 7: 315-332.

PETTS, G. E. & LEWIN, J., 1979. Physical effects of reservoirs on river systems. In *Man's Impact on the Hydrological Cycle in the United Kingdom.* G. E. Hollis, ed., Geo Abstracts, Norwich, 79-91.

PICKERING, T., 1841. *Survey of the River Goulburn from the new to the old Crossing Place with a Tributary Hughes Creek on the East side of it.* Central Plan Office Plan No. Goulburn 60.

PINNINGER, A., 1856. *Map of Part of the upper Goulburn Country.* Central Plan Office Plan No. Goulburn 24.

POWLING, J., 1971. *Limnology of Eildon Reservoir 1969-1970.* State Rivers and Water Supply Commission, Melbourne.

POWLING, J., 1972. *Limnology of Eildon Reservoir 1970-1971.* State Rivers and Water Supply Commission, Melbourne.

POWLING, J., 1980. Limnological features of some Victorian reservoirs. In *An Ecological Basis for Water Resource Management.* W. D. Williams, ed., ANU Press, Canberra, 332-342.

RURAL WATER COMMISSION, undated. *Lake Eildon. Security for Victoria's Irrigation Needs.* Vic. Govt Printer, Melbourne.

SCHUMM, S. A., KHAN, H. R., WINKLEY, B. R. & ROBBINS, L. G., 1972. Variability of river patterns. *Nature (Physical Science)* 23: 75-76.

SHERRARD, J. J. & ERSKINE, W. D., 1991. Complex response of a sand bed stream to upstream impoundment. *Regulated Rivers: Research and Management* 6: 53-70.

SMITH, D. G., 1976. Effect of vegetation on lateral migration of anastomosed channels of a glacier meltwater river. *Geological Society of America Bulletin* 87: 857-860.

SPEEDIE, M. G., 1948. Investigations and designs for Eildon Dam enlargement. *Journal of the Institution of Engineers Australia* 20: 81-91.

STATE RIVERS & WATER SUPPLY COMMISSION, 1981. *Seymour. A Report on Flooding from Goulburn River.* State Rivers and Water Supply Commission, Melbourne.

THOMAS, D. E., 1947. The Geology of the Eildon Dam Project. *Memoir Geological Survey of Victoria No. 16.*

THOMPSON, G. T., 1938. River surveys. *The Australian Surveyor* 7: 28–34.

TURNBULL, C. K., 1957. Taylor's Breakaway: Construction of sheet piling and earth fill overfall structure. *Aqua* 8: 234–238.

WALKER, K. F., 1985. A review of the ecological effects of river regulation in Australia. *Hydrobiologia* 125: 111–129.

WALKER, K. F., HILLMAN, T. J. & WILLIAMS, W. D., 1978. The effects of impoundments on river: an Australian case study. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 20: 1695–1701.

WALKER, P. H. & COVENTRY, R. J., 1976. Soil profile development in some alluvial deposits of eastern New South Wales. *Australian Journal of Soil Research* 14: 305–317.

WILLIAMS, G. P. & WOLMAN, M. G., 1984. Downstream effects of dams on alluvial rivers. *U.S. Geological Survey Professional Paper 1286.*

WILLING & PARTNERS PTY LTD, 1984. *Master Plan Study Final Report.* Shire of Yea River Improvement Trust, Yea.

WOLMAN, M. G., 1954. A method of sampling coarse river-bed material. *Transactions of the American Geophysical Union* 35: 951–956.

WOLMAN, M. G. & LEOPOLD, L. B., 1957. River flood plains: some observations on their formation. *U.S. Geological Survey Professional Paper 282-C.*

WOLMAN, M. G. & MILLER, J. P., 1960. Magnitude and frequency of forces in geomorphic processes. *Journal of Geology* 68: 54–74.

STUDIES ON WESTERN AUSTRALIAN PERMIAN BRACHIOPODS 13. THE FAUNA OF THE ARTINSKIAN MINGENEW FORMATION, PERTH BASIN

N. W. ARCHBOLD

School of Aquatic Science and Natural Resources Management, Deakin University, Rusden Campus, 662 Blackburn Road, Clayton, Victoria 3168, Australia

ARCHBOLD, N. W., 1996:09:30. Studies on Western Australian Permian Brachiopods 13. The fauna of the Artinskian Mingenew Formation, Perth Basin. *Proceedings of the Royal Society of Victoria* 108 (1): 17–42. ISSN 0035-9211.

The brachiopod fauna of the Mingenew Formation, Perth Basin, Western Australia is reviewed and described. The following new taxa are documented: *Strophalosia enantiensis* sp. nov., *Echinalosia simpsoni* sp. nov., *Taeniothaerus roberti* sp. nov., *Coolkilella maitlandi* sp. nov., *Cundaria aquilaformis* gen. et. sp. nov., *Syrella occidenta* gen. et. sp. nov. and *Crassispirifer mingenewensis* sp. nov. The age of the fauna, important for the biostratigraphy of the Permian of the Perth Basin, is reviewed and an age of Early Baigendzhinian (Artinskian) is preferred for the Mingenew Formation.

BRACHIOPODS of Late Palaeozoic age have been known from the Mingenew Formation since Robert Etheridge Junior's identification of specimens collected by E. S. Simpson were first published by A. G. Maitland in 1904. Etheridge (1907a) assigned Simpson's collection to the 'Permo-Carboniferous' and compared the aspect of the fauna with that of the fauna of the Permo-Carboniferous of New South Wales. The present review, of larger and better preserved collections than those available to Etheridge, confirms certain links with eastern Australian Permian faunas. In addition the Mingenew fauna possesses distinct Westralian (Archbold 1983a) elements and an endemic component in the fauna restricted to the Perth Basin.

STRATIGRAPHY

The Permian stratigraphy of the northern Perth Basin has been progressively elucidated by such studies as those of Campbell (1910) and Clarke et al. (1951). A comprehensive description of all Permian units then known was provided by Playford et al. (1976). Additional subsurface data has been described by Tupper et al. (1994) and Mory & Iasky (1994) have provided a structural synthesis of the northern Perth Basin. Harris (1994) has provided an interpretation of the regional tectonic synthesis of the Perth Basin. Le Blanc Smith & Mory (1995) and Mory (1995) have summarised recent data on the stratigraphy and sedimentology from the ongoing surface and subsurface mapping project of the Geological Survey of Western Australia. The maps by Mory & Iasky (1995a, 1995b) indicate the principal fossil localities from which material is described and

illustrated in the present investigation (see also Fig. 1).

The Mingenew Formation is known from three main outcrops, respectively at Enanty Hill, the Simpson Knolls (also previously informally known as 'Fossil Hill') and 5 km west of Arrino. The Formation consists of interbedded sandstone and siltstone. The sequence is commonly ferruginous and is faulted within the Urella Fault Zone (Clarke et al. 1951; Playford et al. 1976) and hence is of unknown stratigraphical limits (Le Blanc Smith & Mory 1995). All marine fossils from surface outcrops are preserved as ferruginous internal and external moulds. Impressions of *Glossopteris* leaves are found rarely and these are often in association with marine fossils.

PREVIOUS BRACHIOPOD STUDIES

The first formal descriptions and illustrations of brachiopod specimens from the Mingenew Formation were provided by Etheridge (1907a). His identifications were listed in reports and summaries by Maitland (1904, 1912, 1919), Glauert (1910) and Campbell (1910). A few species were described by Edgell (1965) and Campbell (1965). Previous identifications, including those of Dickins (1956a), were reassessed by Playford et al. (1976: 116). A number of species have subsequently been described or revised by Archbold (1980a, 1981d, 1987) and Archbold & Thomas (1987) with a summary of then known Perth Basin brachiopod faunas being provided by Archbold (1988), including a list of identifications of the Mingenew fauna. An earlier version of this list was used by Skwarko (1993: 92–93).
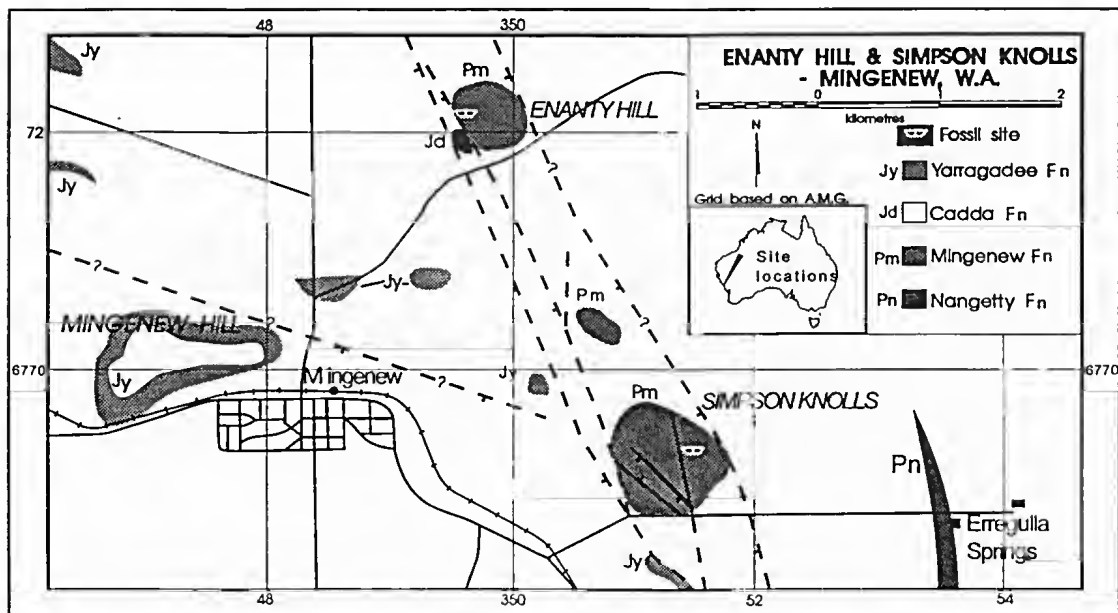
Fig. 1. Locality map of outcrops of Mingenew Formation and fossil localities discussed herein (after Mory & Iasky 1995a, 1995b).

As part of the present study, many of the specimens described by Etheridge (1907a) were re-examined. The specimen (GSWA F227), tentatively referred to *Cyrtina carbonaria* var. *australasica* by Etheridge (1907a: 21), is figured herein (Fig. 9Q, R) and is considered not to be a brachiopod but rather a probable bellerophontid gastropod.

COLLECTIONS AND LOCALITIES

All specimens are registered with the Geological Survey of Western Australia (GSWA F), Perth or with the Commonwealth Palaeontological Collections (CPC) of the Australian Geological Survey Organisation (AGSO), Canberra. All illustrated specimens of new species, other than holotypes, are designated as paratypes.

Material for the present study included elements of E. S. Simpson's original collection from the Simpson Knolls and collections from Enanty Hill and the Simpson Knolls made by subsequent collectors. Material figured and studied by Edgell (1965) from near Arrino was largely re-examined for previous studies (Archbold 1981d, 1987; Archbold & Thomas 1987). Specific collection localities are described as follows.

Enanty Hill. AGSO locality GB53, Enanty Hill, 85 m (280 feet) above base of section, approximately 2.4 km (1.5 miles) north-north east of Mingenew, 29°10′S,115°27′E. GSWA locality 112518, Enanty Hill, west side.

Simpson Knolls. AGSO locality GB52, approximately 2.4 km (1.5 miles) east of Mingenew, 29°12′S,115°28′E, stratigraphical position uncertain. AGSO locality PB15, south side of 'Fossil Hill', Eregulla Springs Station. GSWA collection of E. S. Simpson labelled 2.4 km (1.5 miles) due east of Mingenew Railway Station, on the west and south sides of low hill. GSWA locality 112519, north east, Simpson Knolls, next to track running from access road to Eregulla Farms. Examination of the Simpson Knolls Outcrops of the Mingenew Formation by the author and Dr S. K. Skwarko during November 1988 and the similar type of preservation of all specimens from the Simpson Knolls, indicates that all these localities refer to the same outcrop on the southwestern aspect of the eastern most hill of the Simpson Knolls.

AGE AND CORRELATION OF FAUNA

The faunas of the three known outcrop sites of

the Mingenew Formation are listed in Table 1 for comparison. Each site yields distinctive elements but sufficient forms link the three sites for the faunas to be treated as a whole when considering their age. The most diverse assemblage is from the Simpson Knolls. Differences of the fauna between the three localities probably reflect differences in facies (the Simpson Knolls lithology is sandier than the lithologies of the other localities) and availability of collections.

The fauna of the Mingenew Formation has long been considered to be a correlative of that of the Madeline (Coyrie) Formation of the Carnarvon Basin and the Carynginia Formation elsewhere in the northern Perth Basin (Dickins 1956, 1965; Playford et al. 1976; Archbold 1988, 1993a). While a correlation with the Early Baigendzhinian Lower Byro Group of the Carnarvon Basin is indicated, precise correlation with the Carnarvon Basin

brachiopod zones (*Echinalosia prideri* Zone, *Wyndhamia colemani* Zone, and *Fusispirifer byroensis* Zone) proposed by Archbold (1993a) is premature. *Echinalosia simpsoni* sp. nov. at Enanty Hill and the Simpson Knolls suggests correlation of these sites with the *Echinalosia prideri* Zone of the lower part of the Madeline Formation whereas *Fusispirifer byroensis* from near Arrino may suggest a slightly younger correlation with the *Wyndhamia colemani–Fusispirifer byroensis* Zones of the Carnarvon Basin. However, precise correlation is hampered by the endemicity of many of the Mingenew Formation species and genera.

The Mingenew fauna represents the youngest known Permian marine brachiopod assemblage to crop out in the Perth Basin but a younger early Late Permian assemblage occurs subsurface southwest of Mingenew, west of the Irwin Terrace (Archbold 1995a).

Species	Enanty Hill	Simpson Knolls	Near Arrino
Streptorhynchus sp.	—	✓	—
Tornquistia sp. cf. *T. magna* Archbold 1980	—	✓	—
Neochonetes (Sommeriella) robustus Archbold 1981	—	—	✓
Strophalosia enantiensis sp. nov.	✓	—	✓
Echinalosia simpsoni sp. nov.	✓	✓	—
Mingenewia anomala Archbold 1980	—	✓	—
Taeniothaerus roberti sp. nov.	—	✓	✓
Coolkilella maitlandi sp. nov.	✓	✓	—
Cundaria aquilaformis gen. et sp. nov.	—	✓	—
Syrella occidenta gen. et sp. nov.	—	✓	—
Fusispirifer byroensis Glauert 1912	—	—	✓
Fusispirifer sp.	—	✓	—
Neospirifer sp.	✓	✓	—
Crassispirifer mingenewensis sp. nov.	—	✓	—
Cleiothyridina sp.	—	✓	—
Hoskingia nobilis Etheridge 1907	—	✓	—
Gilledia sp. cf. *G. woolagensis* Campbell 1965	—	✓	—

Table 1. Distribution of brachiopod species between outcrop sites of the Mingenew Formation.

SYSTEMATIC PALAEONTOLOGY

Phylum BRACHIOPODA

Order STROPHOMENIDA Öpik, 1934

Suborder ORTHOTETIDINA Waagen, 1884

Superfamily ORTHOTETOIDEA Waagen, 1884

Family STREPTORHYNCHIDAE Stehli, 1954

Genus Streptorhynchus King, 1850

Type species. *Terebratulites pelargonatus* Schlotheim, 1816.

Streptorhynchus sp.

Fig. 2A–E

Streptorhynchus sp. Archbold 1988: 47.

Comments. One external mould of a dorsal valve (CPC 33852, AGSO locality GB52), one internal mould with external counterpart, of a dorsal valve (GSWA F49466, GSWA locality 112519, width 27 mm, length 21 mm, hinge width 19.3 mm) and one external mould, with internal counterpart, of a ventral valve (GSWA F49467, GSWA locality 112519, length 23 mm) indicate the presence of *Streptorhynchus* within the Mingenew fauna. Dorsal cardinalia and muscle field are typical of the genus. Costellae are fine, equidimensional and increase usually by intercalation with 9 per 5 mm at the anterior margin of GSWA F49466. The species belongs to the finely costellated, thin shelled group of Western Australian *Strepto-*

rhynchus recognised by Thomas (1958) and is closest to *S. johnstonei* Thomas in terms of general shell morphology. However, that Kungurian species from the Coolkilya Formation of the Carnarvon Basin possesses finer costellae than the present material. The specimens from the Mingenew fauna represent a possible ancestral species to *S. johnstonei.*

Order CHONETIDA Nalivkin, 1979

Suborder CHONETIDINA Muir-Wood, 1955

Superfamily ANOPLIOIDEA Muir-Wood, 1962

Family ANOPLIIDAE Muir-Wood, 1962

Genus **Tornquistia** Paeckelmann, 1930

Type species.   Leptaena (Chonetes) polita M'Coy, 1852.

Tornquistia sp. cf. **T. magna** Archbold, 1980

Fig. 2F, G

cf. *Tornquistia magna* Archbold, 1980a *(partim)*: 186, pl. 25, figs 5–8, 10–12 *(non cet.)*—Archbold et al. 1993: pl. 26, figs 6–8.
Tornquistia sp. Archbold 1988: 47.

Comments.   A single internal mould of a dorsal valve with portion of the external mould of the ventral valve exposed (CPC 33853, AGSO locality GB52, ventral valve width 8.3 mm, ventral valve length 5.4 mm) is closely comparable with specimens of *Tornquistia magna* Archbold (1980a) from the Baigendzhinian Bulgadoo Shale of the Carnarvon Basin. The internal dorsal septa and rows of papillae and the shell dimensions are comparable, however, the Mingenew Formation specimen is less concavo-convex than many of the Bulgadoo Shale specimens. A close relationship is indicated but further material is required for a firm species assignment.

Superfamily CHONETOIDEA Bronn, 1862

Family RUGOSOCHONETIDAE
Muir-Wood, 1962

Subfamily RUGOSOCHONETINAE
Muir-Wood, 1962

Genus **Neochonetes** Muir-Wood, 1962

Subgenus **Neochonetes (Sommeriella)**
Archbold, 1982

Type species.   Chonetes prattii Davidson, 1859.

Neochonetes (Sommeriella) robustus
Archbold, 1981

Neochonetes (Sommeria) robustus Archbold 1981: 119, fig. 7A–T, (with synonymy).
Neochonetes (Sommeria) robustus Archbold 1988: 47.—Skwarko 1993: 92.—Archbold et al. 1993: pl. 26, figs 18–20.

Comments.   Edgell (1965: 65, pl. 34, fig. 2) referred several small specimens of *Neochonetes* from the Mingenew Formation cropping out near Arrino to *Chonetes prattii* Davidson. These specimens were re-examined by Archbold (1981: 121, fig. 7N, Q–S) and figured. They were regarded as being juvenile specimens of *N. (S.) robustus* on the basis of their distinct ventral convexity and lack of ventral sulcus. *N. (S.) robustus* is a characteristic species of the Madeline Formation of the Carnarvon Basin.

Order PRODUCTIDA
Sarycheva & Sokolskaya, 1959

Suborder STROPHALOSIIDINA
Waterhouse, 1975

Superfamily STROPHALOSIOIDEA
Schuchert, 1913

Fig. 2. A–E, *Streptorynchus* sp. A, CPC 33852, latex cast of dorsal valve external mould, ×1.2. B–D, GSWA F49466, latex cast of dorsal valve external mould, dorsal valve internal mould and latex cast of dorsal valve internal mould, ×1. E, GSWA F49467, latex cast of ventral valve external mould, ×1. F, G, *Tornquistia* cf. *magna* Archbold, 1980, CPC 33853, internal mould of dorsal valve and latex cast from mould, ×6. H–N, *Mingenewia anomala* Archbold, 1980. H, CPC 33866, latex cast of dorsal external mould, ×4.5. I, CPC 33867, latex cast of dorsal external mould, ×4.5. J, CPC 33870, ventral valve internal mould, ×4.5. K, L, CPC 33871, ventral valve internal mould in ventral and posterior views, ×4 and ×4.5. M, CPC 33872, ventral valve internal mould, ×4.5. N, CPC 33868, latex cast of dorsal valve interior, ×4.5. O–S, *Strophalosia enantiensis* sp. nov., CPC 33854, internal mould of conjoined shell in dorsal and ventral views, ×1.3, latex cast of dorsal valve external mould, ×1.5, latex cast of dorsal interior, ×1.3, dorsal valve external mould, ×1.5.
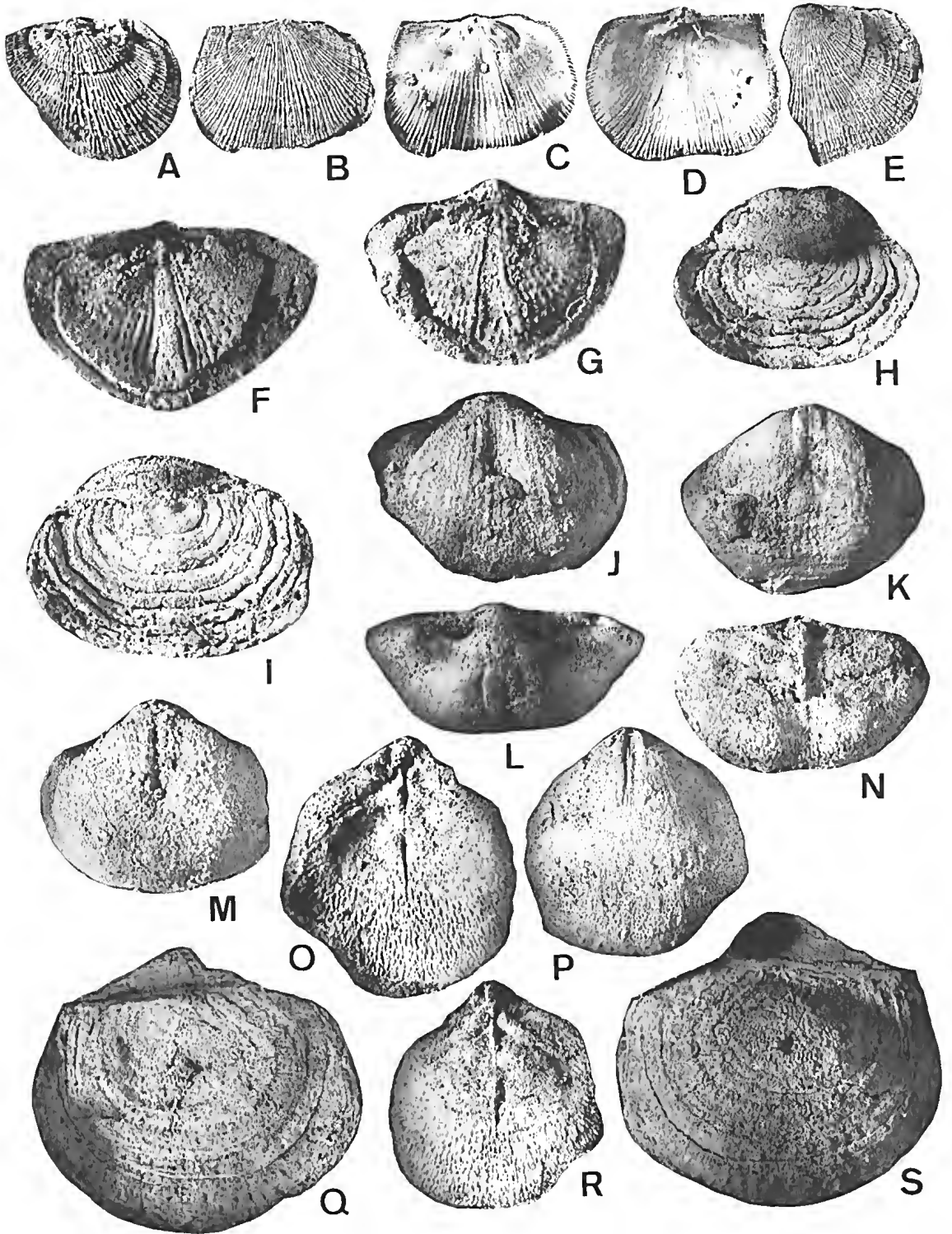
Family STROPHALOSIIDAE Schuchert, 1913

Subfamily STROPHALOSIINAE
Schuchert, 1913

Genus **Strophalosia** King, 1844

Type species. *Strophalosia gerardi* King, 1846.

Comments. The generic definition of *Strophalosia* and the nature of its type species have been subject of considerable discussion as reviewed by Archbold (1986). Species of *Strophalosia* are well known from the Early Permian of Western Australia (Archbold 1986, 1991a; Archbold & Shi 1993; Archbold et al. 1993) and Tasmania (Clarke 1990, 1992). The new species *Strophalosia enantiensis* is the youngest species yet to be recorded from the Permian of Australia.

Strophalosia enantiensis sp. nov.

Fig. 2O–S

Wyndhamia? sp. A, Archbold 1987: 27, fig. 3N, O.
Strophalosia sp. Archbold 1988: 47.
Wyndhamia? sp. Skwarko 1993: 92.

Etymology. From Enanty Hill near Mingenew township.

Holotype. CPC 33854, from AGSO locality GB53, an external mould of a dorsal valve and associated ventral interarea and the internal mould of the same shell.

Diagnosis. Large sized *Strophalosia* with moderately gentle concavo-convexity. dorsal exterior with small dimples anteriorly, growth lamellae and traces of capillae anteriorly. Ventral valve without sulcus.

Description. Mature specimens transversely oval, maximum width at midlength. Ventral interarea broadly triangular, delthyrium distinct, filled with prominent, gently convex pseudodeltidium. Ears small, ill defined. Ventral valve moderately gently convex, ventral sulcus absent. Dorsal valve gently concave, increasing in steepness anteriorly. Dorsal interarea low, inconspicuous.

Ventral exterior not known. Dorsal exterior lacks spines but carries strong growth lamellae and scattered, fine dimples anteriorly (2–3 in 5 mm at 25 mm from umbo), dimples being 0.5 to 0.7 mm in diameter. These may reflect relatively fine ventral spines.

Cardinal process fine, arises from thin median septum and broad lateral ridges surrounding small sockets. Median septum extends some 55% of valve length but virtually disappears when passing through adductor scars. Adductor scars differ-entiated as for genus. Brachial ridges poorly known, anterior of valve interior with rows of radiating elongate papillae.

Ventral interior with narrow, long adductor scars and feeble septum posteriorly. Diductor scars weakly impressed but large and feebly striate.

Dimensions of holotype: maximum width 36.2 mm; ventral length 31.5 mm; dorsal length 27.5 mm; hinge width 26 mm; ventral interarea height 4.2 mm; thickness of internal mould 12.5 mm.

Discussion. Although based on limited material, specifically the holotype and the two specimens discussed by Archbold (1987: 27), distinctive morphological features such as the long narrow ventral adductor scars, the fine dorsal septum and small cardinal process and the distinct ventral interarea and low dorsal interarea indicate a new species. *Strophalosia irwinensis* Coleman (1957) of Sterlitamakian age (see also Archbold 1986) is a smaller species with distinct dorsal radial capillae and broad, rounded ventral adductor muscle scars. The larger Aktastinian species *Strophalosia jimbaensis* Archbold (1986), see also Archbold (1991a) and Archbold & Shi (1993) possesses prominent dorsal external dimples, a prominent dorsal median septum, a relatively low ventral interarea and a prominent dorsal interarea and hence is unlike the new species.

Tasmanian Asselian–Sakmarian species have been well described by Clarke (1990, 1992) and possess deeply impressed ventral diductor scars and ventral adductor scars that are broad and on prominent raised platforms. Neither Tasmanian species would be confused with the present material.

Genus **Echinalosia** Waterhouse, 1967

Type species. *Strophalosia maxwelli* Waterhouse, 1964.

Echinalosia simpsoni sp. nov.

Fig. 3A–V

?*Cleiothyris macleayana* Etheridge *fil.* 1907a: 21.
Echinalosia sp. nov. Archbold 1988: 47.

Etymology. For Mr E. S. Simpson, Mineralogist and Assayer and the first to collect fossils from the Mingenew Formation.

Holotype. GSWA F225, a dorsal valve external mould collected by E. S. Simpson from the Simpson Knolls and labelled as *Cleiothyris macleayana* and hence presumably the single specimen reported, with a query, as this species by Etheridge (1907a: 21).

Figured material. Two ventral valve internal moulds, collected by E. S. Simpson, both labelled GSWA F223, renumbered GSWA F223/1–223/2; CPC 33855–33859, two internal moulds of shells, one ventral valve internal mould, one incomplete ventral valve external mould and one dorsal external mould all from AGSO locality PB15, CPC 33860–33865, one internal mould of a shell, three ventral valve internal moulds, one ventral valve external mould and one incomplete dorsal valve external mould all from AGSO locality GB52.

Measurements (in mm). e = estimate.

Specimen	Max. width	Ventral height	Dorsal height	Hinge width	Thick-ness
GSWA F225	25.5	—	26.0	—	—
GSWA F223/1	27.8	25.5	—	18.0	13.5e
GSWA F223/2	32.5	23.0	—	20.0e	15.0e
CPC 33855	24.5	26.5	23.0	12.0	12.0
CPC 33856	22.5	23.0	21.0	12.0	12.0
CPC 33857	22.0	18.0	—	—	—
CPC 33859	30.0	—	23.0	—	—
CPC 33860	25.0	24.0	21.5	12.0	7.5
CPC 33861	31.0	26.0	—	—	—
CPC 33862	26.5	25.5	—	15.0	11.0e
CPC 33864	18.5	17.5	—	—	—
CPC 33865	26.0	—	20.0	—	—

Diagnosis. Medium sized *Echinalosia*, transversely oval, circular to sub-trigonal in outline. Ventral spines fine, scattered and erect. Dorsal spines very fine, closely scattered, tending to be in concentric rows exteriorly, erect. Hinge of variable width.

Description. Medium sized for genus, outline transversely oval to sub-trigonal. Ventral valve moderately to strongly convex, with median flattening or shallow sulcus. Hinge line straight, up to two-thirds maximum shell width. Maximum shell width at, or anterior of, mid-length of shell. Ears weakly developed or absent, particularly in more sub-trigonal forms. Cicatrix of variable size judging from internal moulds. Ventral interarea low, delthyrial details poorly known.

Exterior ornament of ventral valve of erect spines. Spines scattered along hinge and scattered over valve in ill-defined concentric rows; closely spaced being 5 to 6 per 5 mm at 15 mm from umbo. Spines usually 0.5 mm wide, spine bases up to 0.8 mm wide.

Dorsal valve external ornament of delicate growth lines and fine spines, more numerous and in concentric rows anteriorly; no evidence of dimples. Some 6 to 7 spines per 5 mm at 20 mm from umbo; spine bases 0.1 to 0.15 mm wide.

Ventral teeth small, sharp, close together. Delthyrium small, narrow. Adductor scars elongate, on gently raised platform, bisected by median groove. Diductor scars large, weakly impressed, flabellate, anteriorly weakly striate. Interior of valve anterior weakly striate. Traces of anterior marginal ridge in mature specimens.

Dorsal interior weakly geniculate. Visceral disc internally gently convex. Dorsal adductor scars smooth, weakly raised on low platform, differentiated into anterior and posterior components. Brachial ridges distinct. Cardinal process quadrilobed internally, supported by strong median septum which extends anteriorly for 60% to two-thirds of valve length. Anterior of valve finely pustulose.

Discussion. *Echinalosia simpsoni* sp. nov. is readily distinguished from the only other Western Australian species of the genus, *Echinalosia prideri* (Coleman 1957), by means of its smaller size and much finer ventral and dorsal spines. Archbold (1986: 113, fig. 5A–Z) reviewed Coleman's species and noted that remapping placed the locality of Coleman's syntypic series within the lower part of the Madeline Formation (now usually referred to the Coyrie Formation) of the Carnarvon Basin.

E. simpsoni sp. nov. belongs to the finely spinose *Echinalosia preovalis* and *Echinalosia maxwelli* group of species from eastern Australia and New Zealand (see descriptions by Maxwell 1954; Waterhouse 1964, 1986b; Dear 1971). However, the Austrazean finely spinose species tend to possess strongly developed ventral and dorsal adductor scars. Dorsal spine sizes, when provided in descriptions, for the eastern Australian species appear slightly coarser than those of *E. simpsoni*.

Subfamily MINGENEWIINAE Archbold, 1980

Genus **Mingenewia** Archbold, 1980

Type species. Mingenewia anomala Archbold, 1980.

Mingenewia anomala Archbold, 1980

Figs 2H–N, 4A–Q

Chonetes, sp. indet. Etheridge *fil.* 1907a: 22, pl. 4, fig. 5.
Mingenewia anomala Archbold 1980b: 255, pl. 1, figs 1–20 (with synonymy). — Archbold 1988: 47. — Archbold et al. 1993: pl. 28, figs 12–15. — Skwarko 1993: 92.

Comments. The initial description of *Mingenewia anomala* was based on 15 specimens. The variable preservation of the syntypic series resulted in several morphological features remaining unclear or in doubt. Additional material from AGSO locality PB15 adds considerably to the initial description. Illustrated specimens are CPC 33866–33876 being

two dorsal valve external moulds, two dorsal valve internal moulds, three ventral valve internal moulds, two internal moulds of conjoined shells, one external mould of a ventral valve showing the cardinal area and a ventral external mould with traces of growth lamellae. Material recently collected by Dr A. J. Mory of the Geological Survey of Western Australia from locality GSWA 112519 and illustrated herein includes specimens GSWA F49468–49471, a dorsal valve external mould, two dorsal valve internal moulds and a ventral valve internal mould.

Numerous, but incomplete, external moulds of ventral valves indicate a smooth exterior with no cicatrix of attachment and no ventral body spines or spines along the hinge line. One ventral external mould, CPC 33876, possesses traces of growth lamellae but they are not strongly frilled like those of the dorsal valve. Clear evidence now exists for the presence of a ventral interarea which is low and curved with a broad delthyrium. Teeth are short, curved and separated from the interarea by distinct delthyrial grooves.

The dorsal median septum is significantly thickened for the size of the shell and supports a long-shafted internally bilobed cardinal process that projects slightly ventrally. The cardinal process is essentially spike-like. The dorsal septum bisects the adductor muscle scars which are not differentiated into anterior and posterior pairs unlike those of many strophalosiids. Other features are as described by Archbold (1980b).

No other species of *Mingenewia* has been described but a Late Permian species was reported from Nepal by Waterhouse & Shi (1991: 382).

Suborder PRODUCTIDINA Waagen, 1883

Superfamily AULOSTEGOIDEA
Muir-Wood & Cooper, 1960

Family AULOSTEGIDAE
Muir-Wood & Cooper, 1960

Subfamily AULOSTEGINAE
Muir-Wood & Cooper, 1960

Genus **Taeniothaerus** Whitehouse, 1928

Type species. *Productus subquadratus* Morris, 1845.

Taeniothaerus roberti sp. nov.

Fig. 5A–J

Productus subquadratus—Etheridge *fil.* 1907a: 21, pl. 3, figs 1, 6 (not 6, 7 as in text).
Aulosteges baracoodensis—Edgell 1965: 66, pl. 34, fig. 3.
Taeniothaerus miniliensis—Playford et al. 1976: 116.
Taeniothaerus sp. nov. Archbold 1988: 47.
Aulosteges lyndonensis—Skwarko 1993: 92.

Etymology. For Robert Etheridge Junior who first observed this species from the Mingenew Formation.

Holotype. CPC 33877, an incomplete internal mould of a conjoined shell from AGSO locality GB52.

Figured material. GSWA F224, the original specimen collected by E. S. Simpson and illustrated by Etheridge (1907a: pl. 3, figs 1, 6) from the Simpson Knolls. CPC 33878–33880, an incomplete external mould of a dorsal valve and two incomplete internal moulds of ventral valves from AGSO locality GB52.

Diagnosis. Moderately large *Taeniothaerus* with very low ventral interarea, fine ventral and dorsal spines, rounded ears, distinct ventral sulcus and large, circular dorsal adductor muscle scars.

Description. Moderately large *Taeniothaerus*, slightly elongate, maximum width within the posterior third of the shell. Ventral umbo distinct, pointed, rounded shoulders, overhangs low interarea. No evidence of cicatrix distorting umbo. Ventral valve strongly convex with steep lateral flanks. Sulcus arises some 20 mm from umbo, remains relatively narrow and deepens anteriorly. Interarea low, 1.5–2.5 mm in height on two available specimens. Ventral body spines poorly known but apparently relatively fine and closely spaced. Fine spine bases close to umbo.

Fig. 3. A–U, *Echinalosia simpsoni* sp. nov. A, B, CPC 33855, internal mould of conjoined shell in ventral and dorsal views, ×1.4. C, D, CPC 33860, internal mould of conjoined shell in dorsal and ventral views, ×1.4. E, F, GSWA F223/1, internal mould of ventral valve in ventral and posterior views, ×1.3. G, CPC 33864, latex cast from ventral valve external mould, ×1.3. H, CPC 33858, latex cast from ventral valve external mould, ×1.3. I, J, CPC 33861, ventral valve internal mould in ventral and anterior views, ×1.3. K, L, GSWA F223/2, ventral valve internal mould in anterior and posterior views, ×1.3. M, CPC 33857, ventral valve internal mould, ×1.4. N, O, CPC 33862, ventral valve internal mould in ventral and posterior views, ×1.2 and 1.3. P, CPC 33863, ventral valve internal mould in anterior view, ×1.3. Q, GSWA F225, holotype, dorsal valve external mould, ×1.3. R, T, CPC 33856, internal mould of conjoined shell in ventral view and latex cast of dorsal interior, ×1.3 and ×1.2. S, CPC 33859, dorsal valve external mould, ×1.3. U, CPC 33865, incomplete dorsal valve external mould, ×1.3.
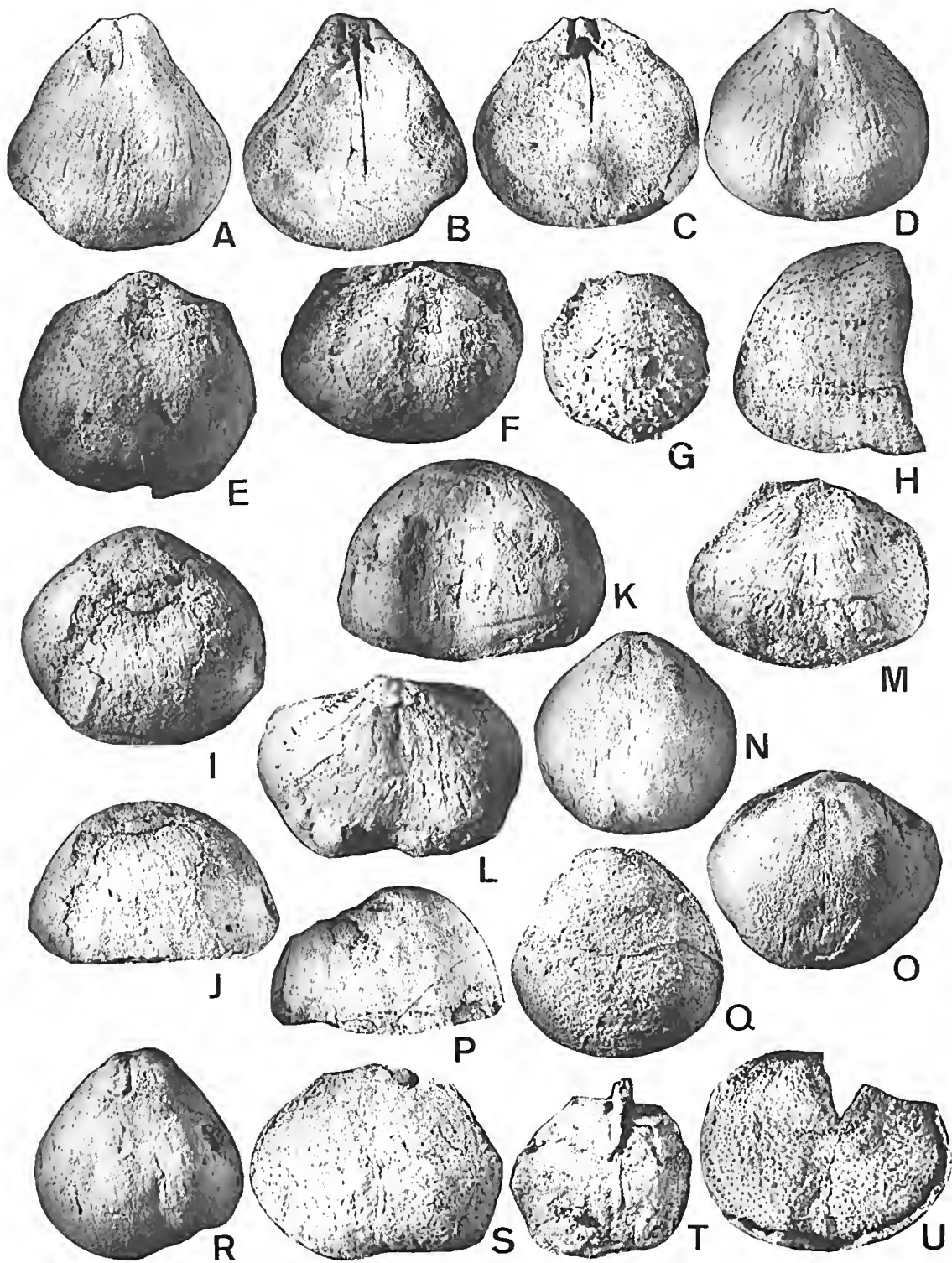
Dorsal valve flat in region of visceral disc with distinct geniculation anteriorly. Spines fine and closely scattered, coarsening slightly anteriorly. Trace of dorsal interarea, less than 1.0 mm high.

Ventral interior with large, striate, flabellate, impressed diductor muscle scars. Adductor scars on weakly raised platform, essentially smooth.

Cardinal process prominent, supported on thick shaft. Shaft is bisected by a deep elongate pit which does not reach process. Cardinal process trilobed with grooved median lobe. Median septum prominent, thickened, bisects adductor muscle field which is almost circular but weakly divided into anterior and posterior components both of which are coarsely striate.

Discussion. Despite the incomplete nature of the material to hand, sufficient distinctive features indicate a new species. The very low ventral interarea, the lack of a deformed ventral umbo and the details of the cardinal process differentiate *T. roberti* sp. nov. from species of *Aulosteges* from the Early Baigendzhinian of the Carnarvon Basin such as *A. ingens* and *A. lyndonensis* (see Coleman 1957; Archbold et al. 1993). Larger species referred to *Taeniothaerus* from Late Baigendzhinian stratigraphical units of the Carnarvon and Canning Basins possess prominent ears, highly differentiated cardinal processes and massively thickened dorsal valves. Spines on most Western Australian Early Permian species are fine except for the poorly known Tastubian species (Archbold 1995b).

Eastern Australian Artinskian *Taeniothaerus subquadratus* (Morris 1845) as redescribed by Parfrey (1983) possesses relatively coarse ventral spine bases, highly differentiated dorsal adductor scars, with their anterior portions smooth, and a prominent groove bisecting the internal face of the cardinal process. The sulcus of *T. subquadratus* is shallow and broad (see also Waterhouse et al. 1983, pl. 1, fig. 11). *T. homevalensis* Briggs (in Waterhouse et al. 1983) possesses a cardinal process closer to that of *T. roberti* sp. nov. but the dorsal

adductor scars of *T. homevalensis* are not circular and the ventral adductor scars are in a prominent elongate raised platform. The sulcus of *T. homevalensis* is not as deep as that of the new species. *T. anotos* Briggs (in Waterhouse et al. 1983) is a highly curved form with a strongly arched shell, unlike *T. roberti* sp. nov.

Superfamily LINOPRODUCTOIDEA Stehli, 1954

Family LINOPRODUCTIDAĒ Stehli, 1954

Subfamily AURICULISPININAE Waterhouse, 1986

Genus **Coolkilella** Archbold, 1993b

Type species. *Cancrinella coolkilyaensis* Archbold, 1983.

Coolkilella maitlandi sp. nov.

Fig. 6A–P

?*Productus undatus*—Etheridge 1907a: 19.
Cancrinella sp.—Playford et al. 1976: 116.
Cancrinella sp. nov.—Archbold 1988: 47.
?*Cancrinella* spp.—Skwarko 1993: 92.

Etymology. For A. Gibb Maitland who, as Government Geologist (Director of the Geological Survey of Western Australia), showed wisdom in sending E. S. Simpson's collection of Mingenew fossils to R. Etheridge Junior for description.

Holotype. GSWA F223/3, an external mould of a dorsal valve and a partial internal mould of the associated conjoined shell, from E. S. Simpson's original collection from the Simpson Knolls.

Other figured material. GSWA F223/4–223/9, one external mould of a dorsal valve and associated internal mould of conjoined shell, two external moulds of dorsal valves, one internal mould of a ventral valve and two external moulds of ventral valves, all from E. S. Simpson's original collection from the Simpson Knolls.

Fig. 4. A–Q, *Mingenewia anomala* Archbold 1980.   A–C, CPC 33873, latex cast of dorsal interior and internal mould of conjoined shell in dorsal and ventral views, ×4.2. D–F, CPC 33874, dorsal interior, latex cast of dorsal interior, and ventral view of internal mould of conjoined shell, ×4.2. G, H, GSWA F49469, latex cast of dorsal interior and dorsal valve internal mould, ×4.2. I, N, GSWA F49470, latex cast from dorsal internal mould, internal and lateral views, ×4 and ×5. J, L, GSWA F49471, latex cast from posterior of ventral valve internal mould and internal mould, ×3.5 and ×4. K, GSWA F49468, latex cast of dorsal valve external mould, ×5. M, CPC 33876, latex cast from ventral valve external mould, ×4.2. O, P, CPC 33875, latex cast from ventral valve mould and detail of interarea, ×4.2 and ×5. Q, CPC 33869, latex cast from dorsal valve internal mould, ×4.
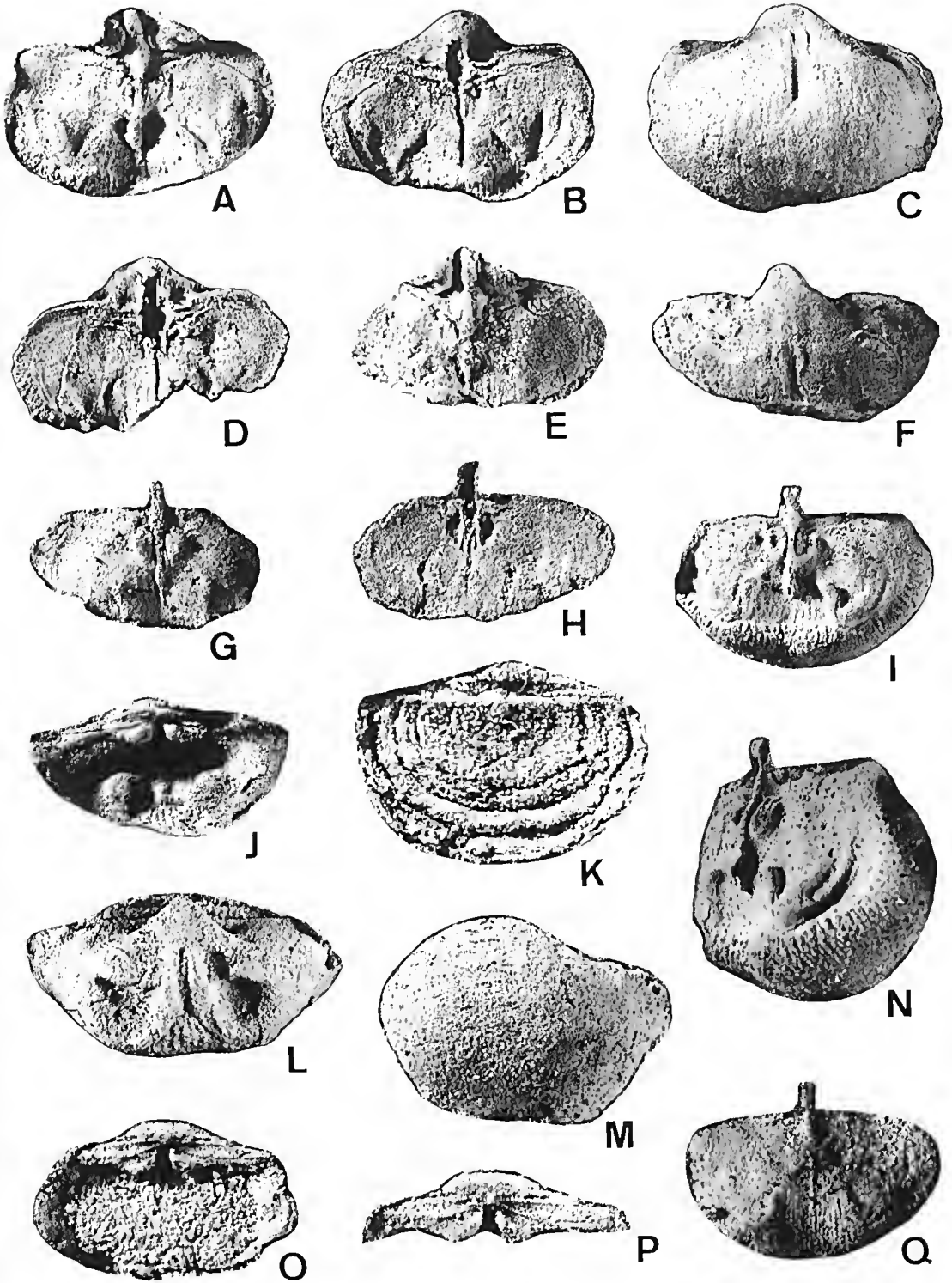
Diagnosis. Average sized *Coolkilella*, moderately convex ventral valve, rugae virtually absent on body of ventral valve, ventral spines fine, costellae moderately fine. Ears rugose.

Measurements (in mm). e = estimate.

Specimen	Maximum width	Ventral height	Dorsal height	Hinge width
GSWA F223/3	26.0	27.5	22.5	–
GSWA F223/4	26.0	–	21.0	16.0e
GSWA F223/5	24.0e	–	20.5	17.5e
GSWA F223/6	–	–	19.5	–
GSWA F223/9	21.5	21.0	–	–

Description. Average sized *Coolkilella*, subcircular to transverse in outline. Maximum width greater than hinge width. Shell surface marked by concentric rugae, poorly developed on ventral valve, fine and low on dorsal valve, distinct on ears. Costellae rounded with narrow interspaces, about 2 to 2.5 per mm at 1.5 cm from umbo. Ventral spines arranged in double row on ears (judging from arrangement of dimples on ears of dorsal valves); body spines arise from elongate swellings on costellae, suberect, extend anteriorly at low angle to shell surface. Dorsal valve with weakly developed rugae over visceral disc, strongly developed over trail, with distinct costellae and prominent elongate dimples.

Profile of ventral valve moderately convex. Ventral umbo small, sharp, overhangs dorsal umbo.

Dorsal valve gently concave on visceral disc, abruptly geniculate anteriorly at maturity, up to 110° from plane of visceral disc.

Ventral interior with external ornament weakly impressed anteriorly. Posterior with low, narrow median ridge for adductor muscle attachment.

Dorsal interior with median septum. Muscle scars weakly impressed in ray like pattern over posterior third of valve interior. Cardinal process bilobed with each lobe divided by groove.

Discussion. *Coolkilella maitlandi* sp. nov. is distinguished from the Western Australian Kungurian *C. coolkilyaensis* (Archbold 1983) by means of its virtual absence of rugae over the body of the ventral valve and its finer costellae. Outlines of the two species are similar except *C. coolkilyaensis* is

more elongate at full maturity. *C. bella* (Etheridge 1918), from the Late Baigendzhinian of the Carnarvon and Canning Basins, also lacks rugae over the body of the ventral valve but possesses coarse ventral spine bases and relatively coarse costae (Archbold 1983).

Order SPIRIFERIDA Waagen, 1883

Suborder SPIRIFERIDINA Waagen, 1883

Superfamily SYRINGOTHYRIDOIDEA Fredericks, 1926

Family SYRINGOTHYRIDIDAE Fredericks, 1926

Subfamily PERMOSYRINXINAE Waterhouse, 1986

Genus **Cundaria** gen. nov.

Type species. *Cundaria aquilaformis* sp. nov.

Etymology. For Professor Aldo Cundari of the Universita di Napoli 'Frederico II', a greatly valued friend and teacher.

Diagnosis. Highly transverse permosyrinxinid with bifurcating costae at maturity. Fastigium broad with shallow median groove. Sulcus shallow, one pair of costae on lateral flanks. Anterior fold distinct. Delthyrium broad. Micro ornament of grooves with posterior papillae and anterior pits.

Discussion. The extremely transverse nature of the shell of *Cundaria* gen. nov. separates this genus from most genera included within the Permosyrinxinae as defined by Waterhouse (1986a, 1987). *Primorewia* Likharev & Kotlyar (1978) from the Pospelovskii Horizon Early Permian of Southern Primorye is a large transverse genus with a deeply grooved dorsal fastigium, syrinx-like structure (but not a true syrinx), simple ribs and a micro-ornament of radially elongate papillae. Small *Primorewia* specimens were recorded by Pavlova (1991 in Pavlova et al. 1991) from the Lower Permian of Southern Mongolia. Costae are simple on the Mongolian specimens (see Pavlova 1991: pl. 31, figs 1–3) and externally the specimens appear similar to juvenile *Cundaria* gen. nov.

Fig. 5. A–J, *Taeniothaerus roberti* sp. nov. A, B, J, holotype, CPC 33877, incomplete internal mould of shell in dorsal and ventral views and latex cast of dorsal interior, ×1. C, CPC 33878, latex cast from dorsal valve external mould, ×1. D, G, H, GSWA F224, latex cast of external mould of posterior of ventral valve in posterior and ventral views and internal mould of ventral valve, ×1. E, F, CPC 33879, incomplete internal mould of ventral valve in ventral and posterior views, ×1. I, CPC 33880, internal mould of ventral valve, ×1.
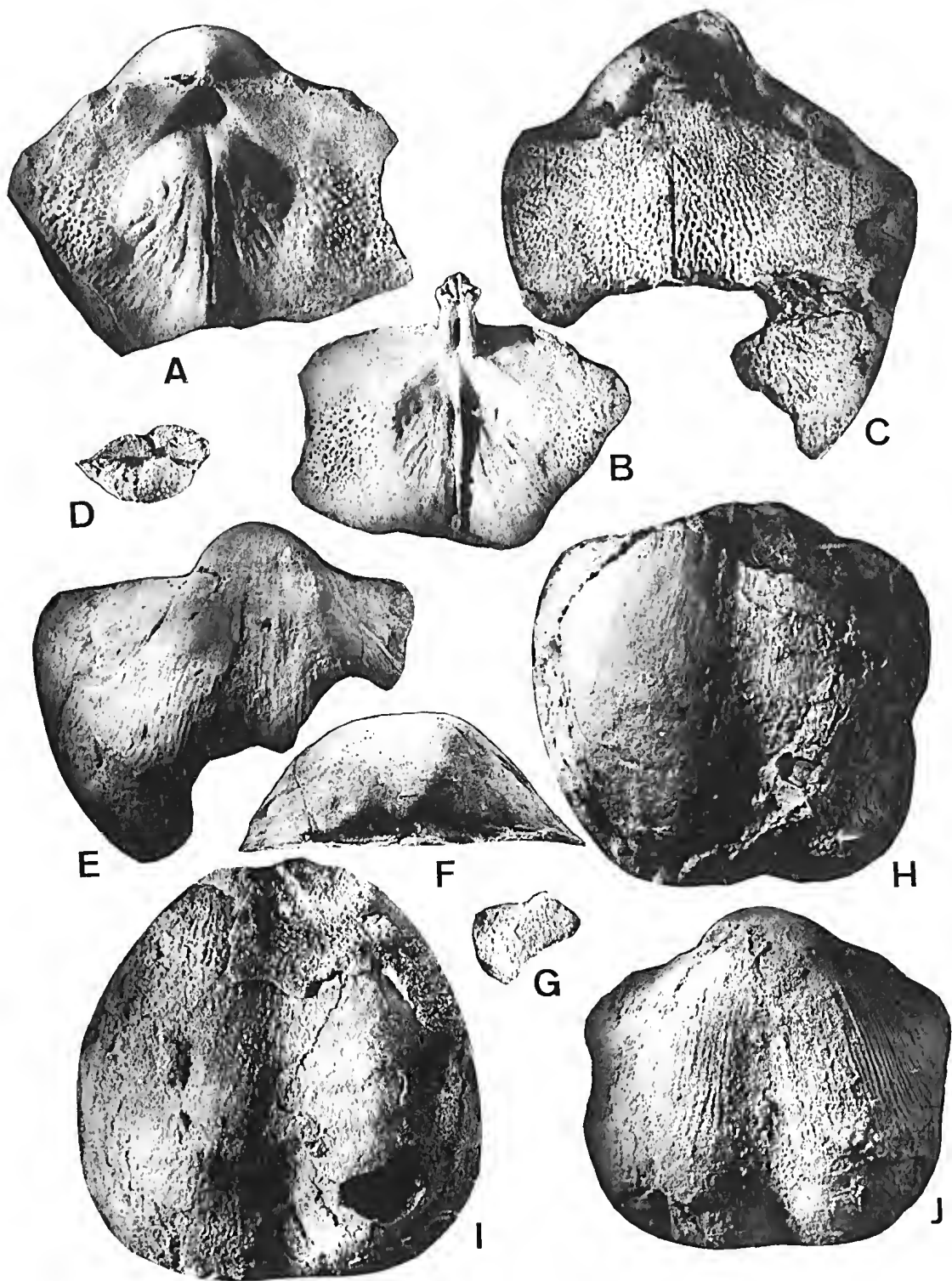
Likharev & Kotlyar (1978) also included within *Primorewia* a specimen figured by Reed (1932: pl. 6, figs 3, 3a) as *Syringothyris nagmargensis*, that possesses an unusual posterior structure in the ventral muscle field. These posterior ventral syrinx-like structures are not present in *Cundaria* gen. nov. *Spirifer nagmargensis* Bion (1928; see also Reed 1932) is usually placed within *Cyrtella* Fredericks (1924), a genus found throughout the Early Permian (Asselian–Sakmarian) of Gondwanan and peri-Gondwanan regions (see Archbold & Gaetani 1993; Angiolini 1995). Type *Cyrtella*, from the Late Artinskian to Ufimian of the Pechora Basin has been reviewed by Grigor'eva et al. (1989).

The most significant feature of *Cundaria* gen. nov. that separates the genus from the various variably transverse forms discussed above is the clear evidence for bifurcating costae on the lateral flanks of both valves, alluded to originally by Etheridge (1915: 29). Occasional bifurcation of costae has been indicated to occur with *Pseudo-syringothyris* Fredericks (1916) by Solomina (1988: 45) and has been illustrated for one specimen of the species *Subansiria granulata* Armstrong (1970: pl. 3, figs 8, 12). Neither report indicates a species comparable with *Cundaria* gen. nov.

Cundaria aquilaformis sp. nov.

Fig. 7A–K

Spirifera avicula—Etheridge *fil.* 1907a: 19, pl. 3, figs 2, 7.
Syringothyris—like *Spirifera*—Etheridge *fil.* 1915: 29, pl. 6, figs 6–8.
Pseudosyrinx sp. cf *P.? sinuosa*—Playford et al. 1976: 116.
permosyrinxinid gen. nov. A—Archbold 1988: 47.
licharewiid gen. nov. A et sp. nov.—Skwarko 1993: 92.

Etymology. In the form or shape of an eagle—an allusion to the extended wings of the genus.

Holotype. GSWA F232/1, an external mould of a dorsal valve with associated ventral interarea and the complete internal mould of the conjoined shell from E. S. Simpson's original collection from the Simpson Knolls.

Other figured material. GSWA F232/2, an external mould of a juvenile dorsal valve and associated ventral interarea, on the same rock specimen as the holotype, from E. S. Simpson's original collection. CPC 33881–33882, an external mould of half a conjoined shell and an external mould of an incomplete dorsal valve and associated ventral cardinal area, from AGSO locality GB52, Simpson Knolls.

Diagnosis. As for genus.

Description. Extremely transverse (holotype estimated 104 mm in width from external mould) with relatively low, apsacline (angle about 160 to 170°) ventral interarea (holotype, estimated length 11.5 mm), shell interior not greatly thickened, external ornament of costae well impressed on internal mould. Fastigium distinct with median groove posteriorly, absent anteriorly; fold distinct at anterior commissure, well rounded. Sulcus relatively shallow, well rounded, minor sulcal tongue. Sulcus broadens to include first pair of lateral flank costae by mid-length of holotype (at about 12 mm).

Juvenile specimens possess very low ventral and dorsal interareas and simple, fine costae near umbones. Costae coarsen rapidly but only holotype internal mould possesses clear evidence of bifurcation of costae on both valves at about 13 mm distance from umbones; this is precisely the distance at which the external mould is broken.

Ventral interior with strong dental plates, adminicula component not greatly thickened. Ventral muscle field between adminicula gently impressed (holotype ventral muscle field 12.5 mm wide, 14 mm long); diductor scars gently striate anteriorly, adductor scars narrow with short, low median ridge posteriorly. Valve interior smooth.

Dorsal interior with distinct socket plates and striate cardinal process (latter being 4.0 mm wide on holotype). Delicate median myophragm arises 4.0 mm anterior of cardinal process and extends anteriorly for 12.0 mm on holotype. Costae up to 17 in number on each lateral flank of holotype at anterior margin; juvenile specimens indicate some 13 or 14 on each flank may be primary costae. Micro-ornament of elongate

Fig. 6. A–P, *Coolkilella maitlandi* sp. nov. A–C, F, N, O, GSWA F223/3, holotype, external mould of dorsal valve in dorsal, antero-dorsal, anterior and profile views and incomplete internal mould of conjoined shell in dorsal view and latex cast of dorsal interior, all ×1.6. D, E, GSWA F223/5, dorsal valve external mould and latex cast of dorsal exterior, ×1.5. G–J, GSWA F223/4, internal mould of conjoined shells in dorsal view, latex cast of dorsal interior, dorsal valve external mould and latex cast of dorsal valve exterior, ×1.5. K, GSWA F223/7, ventral valve internal mould, ×1.4. L, GSWA F223/8, latex cast of ventral valve external mould, ×1.4. M, GSWA F223/6, dorsal valve external mould, ×1.4. P, GSWA F223/9, latex cast of ventral valve external mould, ×1.4.
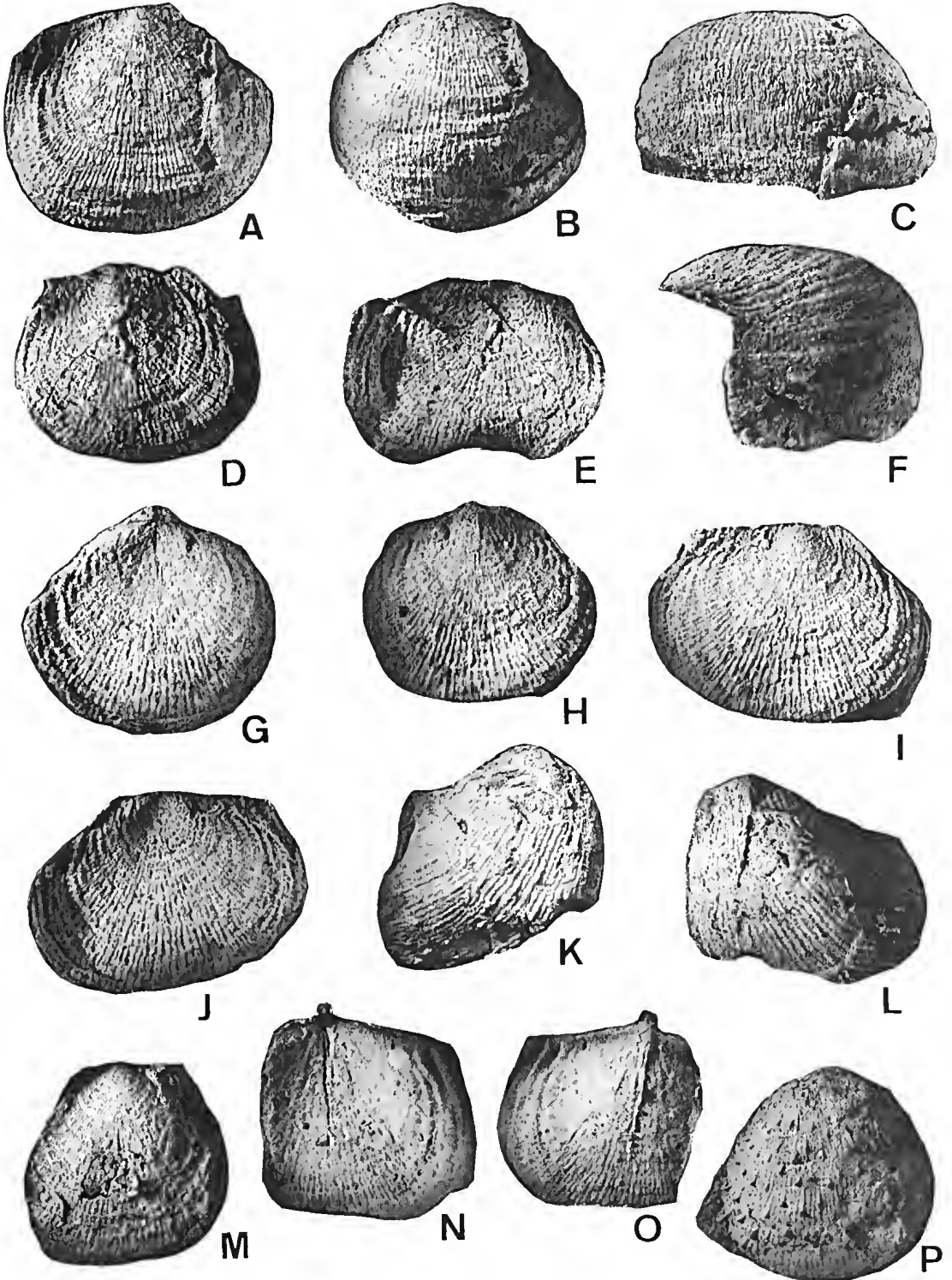
grooves (0.5 to 0.75 mm in length) each with anterior pit and posterior pustule.

Discussion. The distinctive morphology of *Cundaria aquilaformis* sp. nov. appears to be unlike that of other described species within the Permosyrinxinae. The species *Pseudosyrinx*? *sinuosa* Thomas (1971), from the Coyrie Formation of the Carnarvon Basin, to which the present form was referred to by Playford et al. (1976), possesses a highly sinuous anterior commissure, prominent sulcal tongue, extensively thickened shell posterior and simple costae (Thomas 1971; pl. 13, figs 1, 2; pl. 30, figs 6–8). It is not as transverse as the present species. As discussed by Thomas (1971) its generic position is not certain but it is unlikely to be closely related to *Cundaria aquilaformis* sp. nov.

Genus Syrella gen. nov.

Type species. *Syrella occidenta* sp. nov.

Etymology. A combination of syllables from generic names within the subfamily Permosyrinxinae.

Diagnosis. Small permosyrinxinid with transverse, rounded outline, up to 12 pair of costae on lateral flanks at maturity. Ventral interarea of moderate height, weakly to moderately apsacline. Dental plates stout and thickened, adminicula strong, about one-third of valve length. At maturity, ventral muscle field with short posterior calcite rod splitting apex of adductor muscle scars; this may lead anteriorly to low median septum or ridge. Separating adductor scars from the posterior portion of the diductor scars at maturity are two additional sharp rods or septa. These apical structures strengthen during ontogeny (see Fig. 8O, J, L, F). Shell apparently punctate.

Discussion. Genera within the subfamilies Licharewiinae and Permosyrinxinae have received considerable attention from Grigor'eva & Kotlyar (1966), Grigor'eva (1977), Waterhouse (1983a, 1986b, 1987), Solomina (1985, 1988) and Grigor'eva et al. (1989). A range of variations of ventral apical structures, delthyial structures, dental plate arrangements and micro-ornament characteristics are used to separate genera and some questions remain to be answered. The distinction

between *Cyrtella* Fredericks (1924) and *Punctocyrtella* Plodowski (1968) requires final resolution (cf. Grunt 1993) and the nature of the microornament of *Subansiria* Sahni & Srivastava (1956) requires elucidation. Nevertheless, the present form appears to possess a distinctive combination of morphological characters, including the distinctive ventral posterior structures, from other described genera.

Syrella occidenta sp. nov.

Fig. 8A–T

Spirifer sp. ind. Etheridge 1907a: 20, pl. 3, figs 3–5; pl. 6, fig. 6.
Permosyrinxinid gen. nov. B, Archbold 1988: 47.
Licharewiid gen. nov. B sp. nov. A, Skwarko 1993: 92.

Etymology. In reference to western Australia in its distribution.

Holotype. CPC 33883, an internal mould of a conjoined shell and the associated external mould of the dorsal valve and ventral interarea and umbo, from AGSO locality PB15, 'Fossil Hill' (Simpson Knolls).

Other figured material. CPC 33884–33889, five internal moulds of conjoined shells and one incomplete external mould of a ventral valve all from AGSO locality PB15, 'Fossil Hill' (Simpson Knolls).

Measurements (in mm).

Specimen	Max. width	Hinge width	Ventral length	Dorsal length	Thickness
CPC 33883	39.5	35.0	28.5	23.0	—
CPC 33884	37.0	35.0	21.0	19.0	15.0
CPC 33885	31.0	29.0	25.0	20.0	16.5
CPC 33886	31.0+	28.5+	23.5	19.0	15.5
CPC 33887	27.0	24.0	20.0	16.5	15.0
CPC 33888	24.5	22.0	20.0	16.5	15.0

Diagnosis. As for genus.

Description. Transverse, compact relatively thick shells with low to moderate ventral interareas. Shell posterior moderately thickened, anterior of internal moulds with external ornament impressed internally. External ornament of simple costae, up to 12 pair on dorsal lateral flanks of holotype. Fastigium distinct, raised abruptly from lateral flanks, with broad median depression, weakens anteriorly at maturity so fold almost flat at

Fig. 7. *Cundaria aquilaformis* gen. et sp. nov. A–E, holotype, GSWA F232/1, internal mould of conjoined shell in dorsal, ventral and posterior views, latex cast of dorsal exterior and external mould of dorsal exterior, ×1. F–H, CPC 33881, latex cast of incomplete shell in dorsal, ventral and posterior views, ×1.2 and ×1. I, J, CPC 33882, latex cast of dorsal external mould, ×1 and surface detail, ×9. K, GSWA F232/2, latex cast of dorsal external mould, ×1.
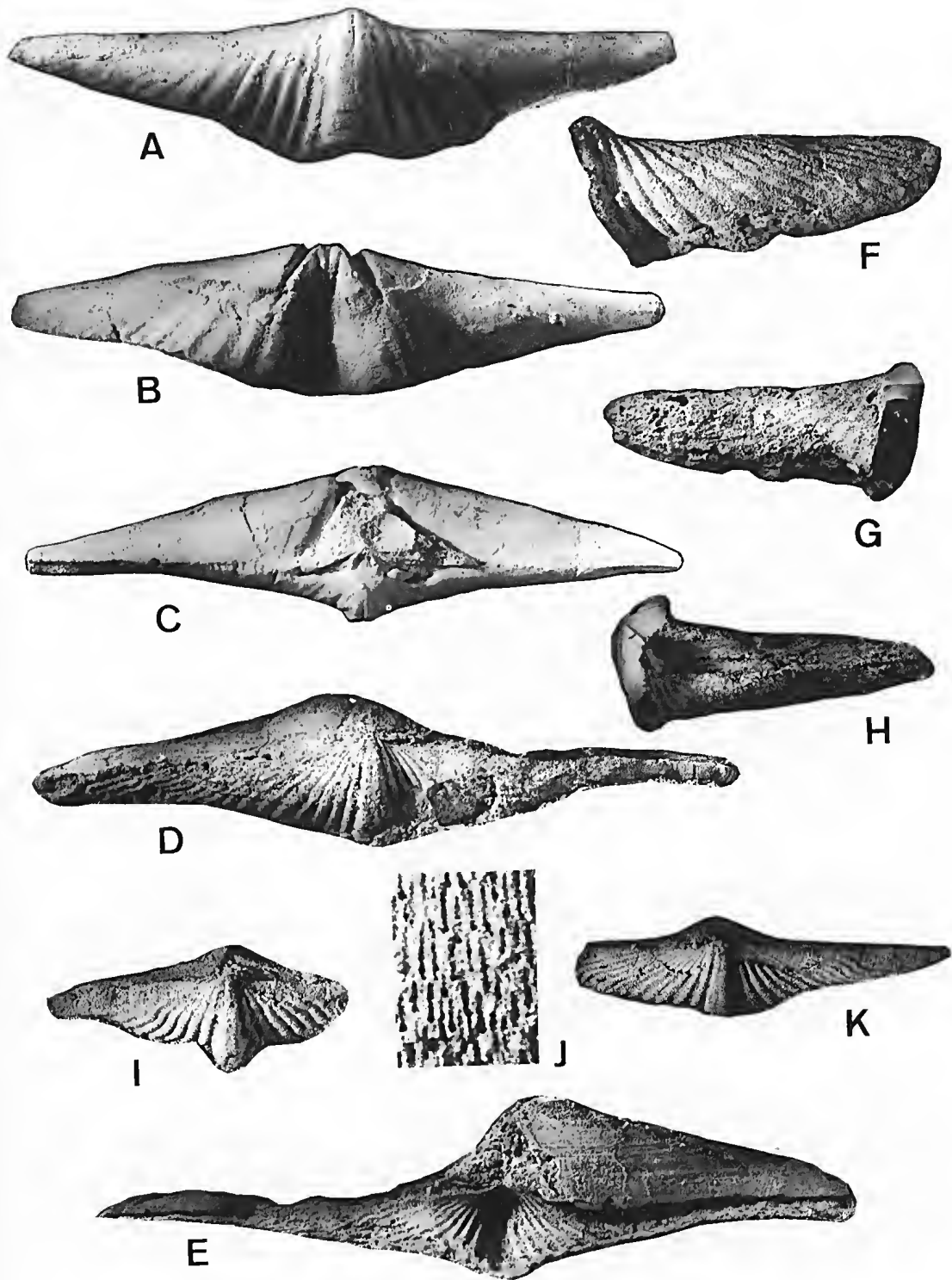
commissure, Sulcus well rounded with prominent anterior sulcal tongue. Fastigium and sulcus smooth.

Ventral interior with strong, stout dental plates. Adminicula stout, thickened, about one-third of valve length. Ventral muscle field equidimensional to slightly elongate, adductor scars occupy long, raised section of muscle field with weakly striate diductors either side. At maturity sharp, blade-like septa, or rods, split posterior of adductor field and demarcate posterior adductors from posterior diductors. On specimen CPC 33885, median septum 3.0 mm long, extending anteriorly as delicate low median myophragm; 'lateral' septa 4.5 mm long (Fig. 8L). Ventral interarea horizontally striate, delthyrium broad with posterior curved delthyrial plate at level of delthyrial grooves.

Dorsal interior with distinct, wide socket plates and striate cardinal process. Delicate, blade-like median septum arises 2 to 3 mm anteriorly of cardinal process and extends anteriorly for 60% of valve length. Dorsal adductor scars distinct, differentiated into anterior and posterior pairs. Anterior pair extends to end of median septum.

Micro-ornament of shell consists of fine elongate grooves with evidence for anterior pits to the grooves and scattered posterior pustules. Fine granulose pits on external mould fragments are taken to indicate punctae.

Discussion. *Syrella occidenta* sp. nov. with its striking septal arrangement at the posterior of its ventral muscle field is a distinctive species. Of eastern Australian permosyrinxinids described by Armstrong (1970) and Waterhouse (1987) only *Subansiria elongata* Armstrong (1970: pl. 2, figs 1–5) possesses weakly developed posterior ventral septa that are comparable to those of the Mingenew Formation species, although not so well developed. Armstrong's Queensland species, from the Artinskian Tiverton Formation, possesses fewer costae at maturity and a pronounced dorsal median septum when compared with *Syrella occidenta* sp. nov. Waterhouse (1987) assigned, with a query, *Subansiria elongata* to *Permosyrinx*.

Superfamily SPIRIFEROIDEA King, 1846

Family SPIRIFERIDAE King, 1846

Subfamily NEOSPIRIFERINAE Waterhouse, 1968

Genus **Fusispirifer** Waterhouse, 1966

Type species. *Spirifer nitiensis* Diener, 1897.

Fusispirifer byroensis (Glauert, 1912)

Fusispirifer byroensis (Glauert)—Archbold & Thomas 1987: 181, figs 3A–H, 4A–F (with synonymy).— *Fusispirifer byroensis*, Archbold 1988: 47.—Archbold ct al. 1993: pl. 40, figs 1–3.—Skwarko 1993: 92.

Comments. The specimen from the Mingcnew Formation that crops out near Arrino and was figured by Edgell (1965: pl. 34, fig. 1), was reviewed and refigured by Archbold & Thomas (1987: 184, fig. 4F). Although incomplete, the specimen is consistent with referral to Glauert's species.

Fusispirifer sp.

Fig. 9A–C, J, K

Comments. A small collection of incomplete specimens is referred to the genus *Fusispirifer* Waterhouse. Figured material includes: GSWA F232/3, an incomplete external mould of a mature ventral valve from E. S. Simpson's original collection from the Simpson Knolls; CPC 33890, an incomplete ventral valve external mould from AGSO locality 'Fossil Hill'; CPC 33891–33892, an incomplete ventral valve internal mould and an incomplete dorsal valve internal mould from AGSO locality GB52, Simpson Knolls.

The available material indicates a large species with a low ventral interarea, distinct delthyrial plate and prominent costae. Costae are sharper and less flattened than those of *Fusispirifer byroensis* (Glauert) and hence the spccimcns are left in open nomenclature.

Fig. 8. A–T, *Syrella occidenta* gen. et sp. nov. A, C–G, holotype, CPC 33883, internal mould of conjoined shell in dorsal, ventral, posterior, postero-ventral and anterior views and latex cast of dorsal valve external mould, A, C, E and G, ×1.25, D, F, ×1. B, O, P, CPC 33888, internal mould of conjoined shell in anterior view, ×1, and ventral and posterior views, ×1.3. H, I, Q, CPC 33884, internal mould of conjoined shell in dorsal view and latex cast of external mould of shell antcrior in dorsal and anterior views, ×1.25. J, K, CPC 33886, internal mould of conjoined shell in ventral and dorsal views, ×1.25 and ×1. L–N, CPC 33885, internal mould of conjoined shell in postero-ventral, ventral and anterior views, ×1.3. R, CPC 33887, internal mould of conjoined shell in dorsal view, ×1.3. S, T, CPC 33889, latex cast of ventral valve external mould, detail of surface and ventral view, ×8 and ×3.5.
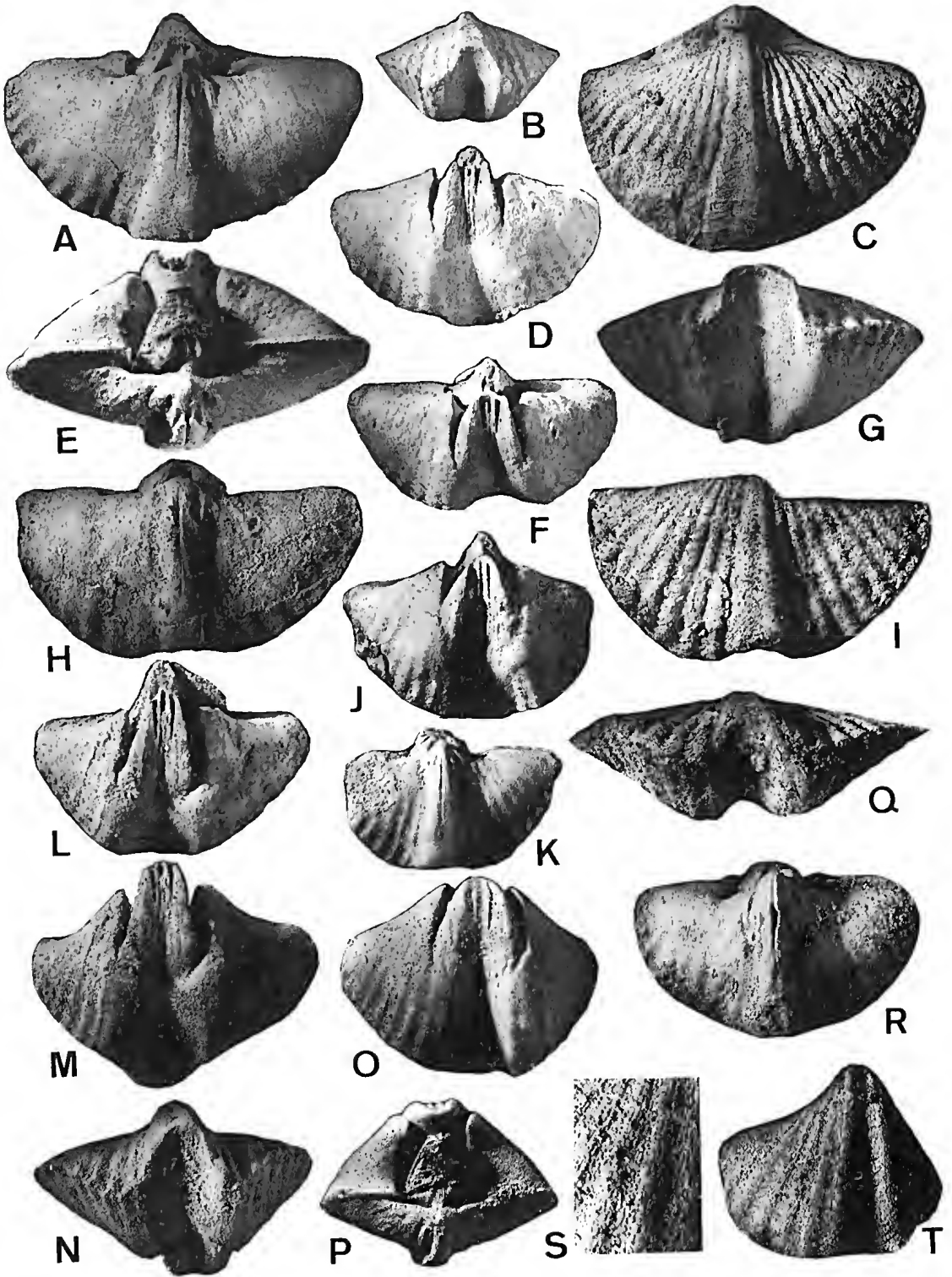
Genus **Neospirifer** Fredericks, 1924

Type species. *Spirifer fasciger* von Keyserling, 1846.

Neospirifer sp.

Fig. 9E–I, L–N

Neospirifer sp. Archbold 1988: 47.

Measurements (in mm). e = estimate.

Specimen	Maximum width	Ventral length	Dorsal length
CPC 33893	41.0e	26.0	16.5
CPC 33894	40.0e	–	21.5
CPC 33895	44.0e	–	15.0+

Comments. Three specimens indicate the presence of a small species of finely costate and plicate *Neospirifer* within the Mingenew fauna. Figured material includes CPC 33893–33895, an incomplete internal mould of a conjoined shell and two incomplete dorsal valve internal moulds both with associated dorsal valve external moulds all from AGSO locality GB52, Simpson Knolls.

Comparison of the specimens with the described species of *Neospirifer* from the Western Australian Permian is hampered by their incomplete preservation but the fine sharp costae, fine lateral plications, relatively high sharp fastigium and the nature of the ventral muscle field does suggest a comparison with juvenile and sub-mature stages of the Early Baigendzhinian Madeline Formation species *Neospirifer plicatus* Archbold & Thomas (1986: figs 5A–K, 6A–I). The Madeline Formation species is variable in terms of ontogeny but belongs to a distinctive group of *Neospirifer* species with high fastigia and truncated hinge lines at maturity. Present material does not provide adequate information on hinge characteristics.

Genus **Crassispirifer** Archbold & Thomas, 1985

Type species. *Spirifer rostalinus* Hosking, 1931.

Crassispirifer mingenewensis sp. nov.

Figs 9D, 10A–L

Holotype. CPC 33896, an internal mould of a conjoined shell and portion of the external mould of the dorsal valve from AGSO locality GB52, Simpson Knolls.

Other figured material. CPC 33897, an internal mould of a ventral valve and counterpart external mould from AGSO locality GB52, Simpson Knolls.

Measurements (in mm). e = estimate.

Specimen	Maximum width	Ventral length	Dorsal length	Thickness
CPC 33896	80.0e	35.0e	35.0	35.5
CPC 33897	98.0e	35.0	–	–

Diagnosis. Strongly plicate, transverse *Crassispirifer* with extremely high fastigium.

Description. Moderate sized species, biconvex, transverse, maximum width at hinge line.

Ventral umbo small, arched over interarea. Interarea moderately high, striated horizontally (growth lines) and, less regularly, vertically (denticular grooves). Delthyrium distinct, delthyial grooves and ridges present. Sulcus arises at umbo, broadens to incorporate first pair of plications. Sulcal tongue prominent. Lateral plications prominent, up to six pairs on valve. Fasciculation of costae distinct, up to six costae per bundle. Costae sharp, equidimensional, intercostal valleys narrow.

Dorsal umbo small, pointed; interarea low. Fastigium arises at umbo, remains sharp and narrow, extremely high. Anterior fold prominent, sharp crested. Lateral plications distinct, costae as for ventral valve.

External micro-ornament strongly tegulate, about 7 growth lamellae at 2 cm from umbones.

Ventral teeth stout, thickened dental flanges supported by short, thickened adminicula. Ventral muscle field longer than wide. Dorsal interior with short, stout socket plates. Cardinal process wider than long.

Fig. 9. A–C, J, K, *Fusispirifer* sp. A, GSWA F232/3, latex cast from ventral valve external mould, ×1. B, CPC 33890, latex cast from ventral valve external mould, ×1. C, CPC 33891, incomplete ventral valve internal mould, ×1. J, K, CPC 33892, incomplete dorsal valve internal mould and latex cast of dorsal interior, ×1. D, *Crassispirifer mingenewensis* sp. nov. CPC 33897, latex cast of external mould of central portion of ventral interarea, ×1. E–I, L–N, *Neospirifer* sp. E–G, CPC 33893, internal mould of conjoined shell in posterior, ventral and dorsal views, ×1.2. H, I, CPC 33894, internal mould of dorsal valve and latex cast of dorsal external mould, ×1.2. L–N, CPC 33895, latex cast of dorsal external mould and dorsal internal mould in postero-dorsal and dorsal views, ×1.2. O, P, *Cleiothyridina* sp. O, CPC 33898, latex cast of ventral? valve external mould, ×1.6. P, CPC 33899, latex cast of dorsal? valve external mould, ×3.5. Q, R, bellerophontid gastropod?, GSWA F227, identified as a possible *Cyrtina carbonaria* var. *australasica* (=*Spiriferella*) by Etheridge (1907a: 21), ×1.2.
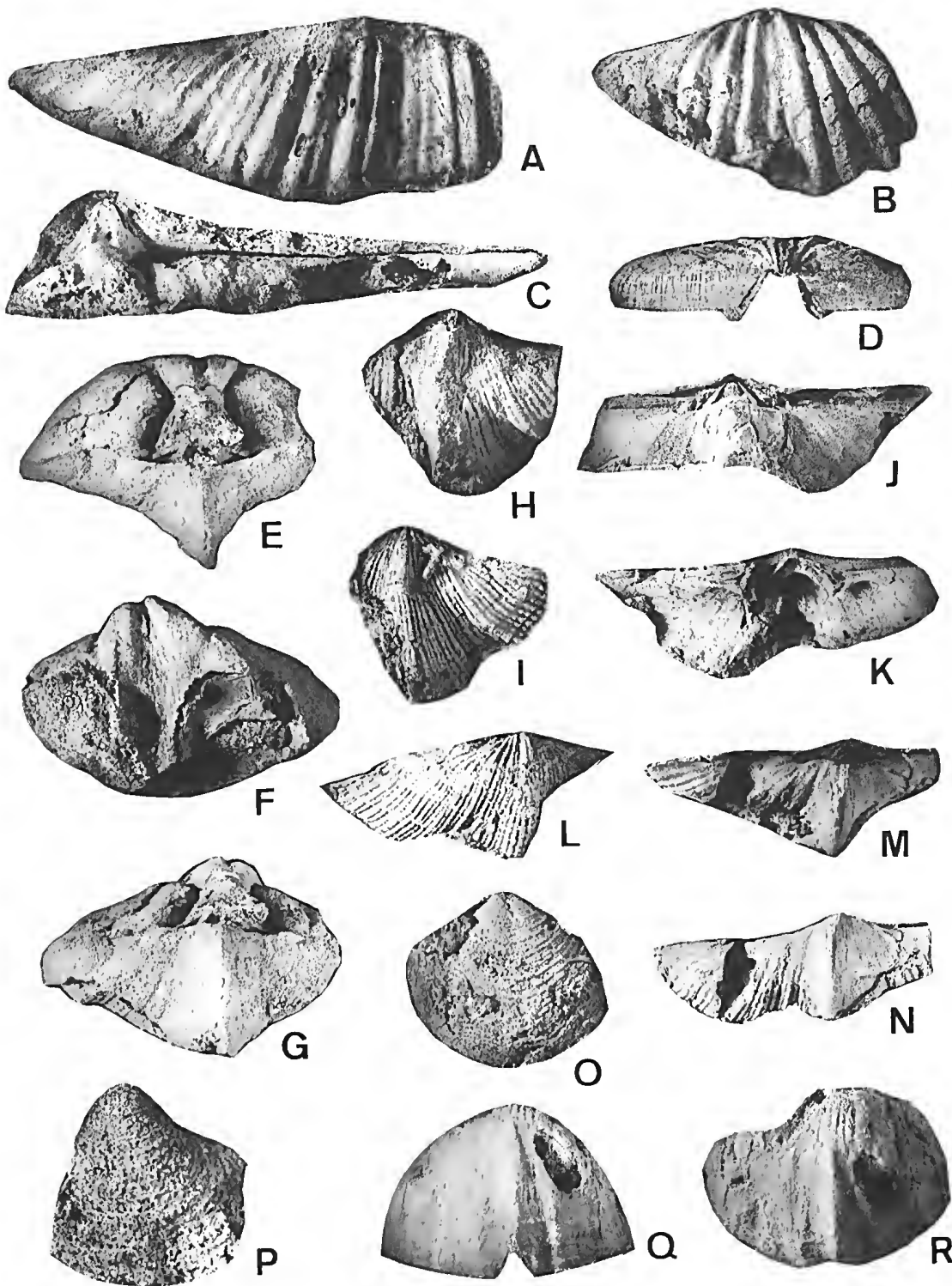
Discussion. *Crassispirifer mingenewensis* sp. nov. is a highly distinct species, easily recognised by its extremely high and narrow dorsal fastigium, long ventral sulcal tongue, prominent lateral plications, sharp, relatively narrow costae and tegulate micro-ornament.

Species of *Crassispirifer* have been described by Archbold & Thomas (1985) from the late Early Permian of Western Australia and Abramov & Grigor'eva (1988) from a range of Permian horizons of the Russian Arctic but these species all lack the striking fastigium of the present species. Archbold & Shi (1993) documented a small species from the Aktastinian of the Carnarvon Basin that also lacks a high, narrow fastigium.

Crassispirifer mingenewensis sp. nov. and a similar new, undescribed species from the High Cliff Sandstone of the Perth Basin species (to be based on extensive well preserved material) will be placed in a new genus when the High Cliff species is described.

Order ATHYRIDIDA Dagys, 1974

Superfamily ATHYRIDOIDEA McCoy, 1844

Family ATHYRIDIDAE McCoy, 1844

Genus **Cleiothyridina** Buckman, 1906

Type species. *Atrypa pectinifera* Sowerby, 1840.

Cleiothyridina sp.

Fig. 9O, P

Cleiothyridina sp. Archbold 1988: 47.
Cleiothyridina sp. Skwarko 1993: 92.

Comments. Two small incomplete specimens (CPC 33898–33899) of external moulds of a ventral? and a dorsal valve from AGSO locality GB52, Simpson Knolls, possess the characteristic concentric lamellae and spine bases of *Cleiothyridina*, or a related genus. Material is inadequate for comparison with described Western Australian species.

Order TEREBRATULIDA Waagen, 1883

Suborder TEREBRATULIDINA Waagen, 1883

Superfamily DIELASMATOIDEA Schuchert, 1913

Family DIELASMATIDAE Schuchert, 1913

Subfamily DIELASMATINAE Schuchert, 1913

Genus **Hoskingia** Campbell 1965

Type species. *Dielasma trigonopsis* Hosking, 1933a.

Hoskingia nobilis (Etheridge, 1907a)

Fig. 11A–K, M

Dielasma nobilis Etheridge *fil.* 1907a: 19, pl. 4, figs 2–4; pl. 6, figs 1, 2.—Crespin 1964: 65.
Hoskingia nobilis Campbell 1965: 59, pl. 12, figs 8–13.— Playford et al 1976: 116.—Archbold 1988: 47.— Archbold et al. 1993: pl. 45, figs 4, 5, 9–11.—Skwarko 1993: 93.

Figured material. GSWA F230 and GSWA F49472-49473, an internal mould of a conjoined submature shell from E. S. Simpson's original collection, an external mould of the dorsal aspect of a conjoined shell and an internal mould of a fully mature conjoined shell, both from GSWA locality 112519, Simpson Knolls. CPC 33900–33902, three internal moulds of conjoined shells from AGSO locality GB52, Simpson Knolls.

Measurements (in mm). e = estimate.

Specimen	Maximum width	Ventral length	Dorsal length	Thickness
CPC 33900	41.0	57.5	51.0	27.5
CPC 33901	33.0	42.0	37.0	22.0
CPC 33902	28.0	36.0	32.0	15.0
GSWA F230	22.0	31.0+	26.5	11.5
GSWA F49472	32.0e	37.0	34.0	—
GSWA F49473	41.0	54.0	45.0	—

Comments. Campbell (1965: 59) described the species in some detail and illustrated two specimens. The present material represents a range of specimens from sub-mature to mature size. Morphology of the species shows little variability between individuals. The external mould reveals delicate growth lines (about 6 per mm at 1.5 mm from umbo) and significant growth lines at longer

Fig. 10. A–L, *Crassispirifer mingenewensis* sp. nov. A, C, E, 1, J, CPC 33897, internal mould of ventral valve in ventral, posterior and postero-ventral views and latex cast of ventral valve external mould in ventral and postero-ventral views, ×1. B, D, F–H, K, L, holotype, CPC 33896, internal mould of conjoined shell in posterior, postero-ventral, ventral, dorsal, postero-dorsal and anterior views, all ×1 except K, ×1.25, and latex cast of incomplete dorsal valve external mould, ×1.
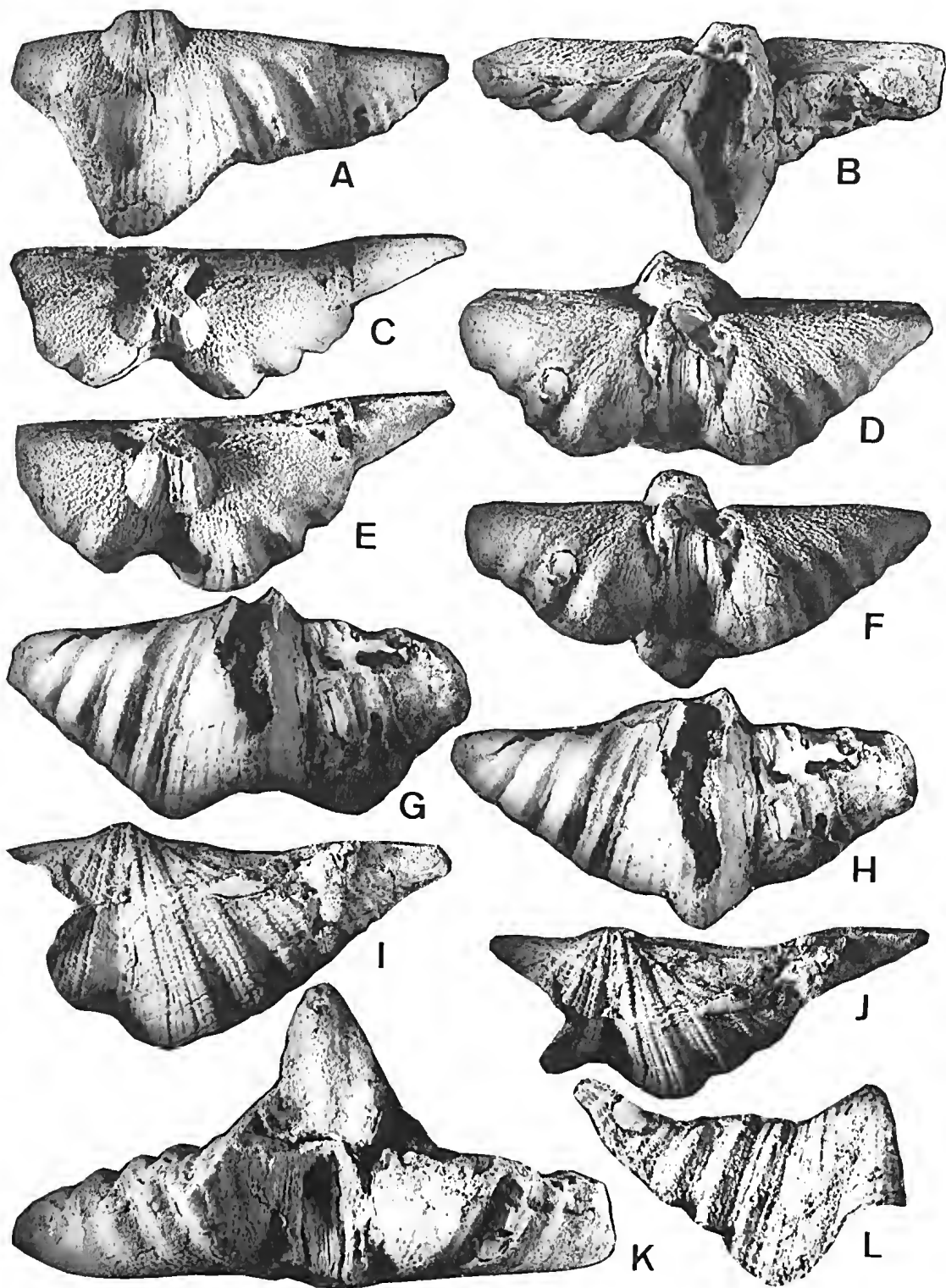
intervals. Punctae are not preserved on the external mould. Both Etheridge (1907a: 20) and Campbell (1965: 60) indicated the distinctive plication pattern of the shell of this species.

Family GILLEDIIDAE Campbell, 1965

Subfamily GILLEDIINAE Campbell, 1965

Genus **Gilledia** Stehli, 1961

Type species. *Terebratula cymbaeformis* Morris, 1845.

Gilledia sp. cf. G. woolagensis Campbell 1965

Fig. 11L, N–R

Gilledia woolagensis Campbell (*partim*) 1965: 82 (*non illus.*). —Playford et al. 1976: 116. —Archbold 1988: 47. —Skwarko 1993: 93.
Gilledia cf. *homevalensis* Campbell (*partim*) 1965: 79. — Archbold 1988: 47. —Skwarko 1993: 93.

Figured material. CPC 33903–33905, three internal moulds of conjoined shells all from AGSO locality PB15, 'Fossil Hill' (Simpson Knolls).

Measurements (in mm).

Specimen	Maximum width	Ventral length	Dorsal length	Thickness
CPC 33903	21.0	28.5	25.0	13.5
CPC 33904	18.5	27.5	24.0	12.5
CPC 33905	17.0	24.0	22.0	11.0

Comments. Campbell (1965: 79, 82) briefly discussed but did not illustrate specimens of *Gilledia* from the Mingenew Formation that he considered to be closely comparable with *G. homevalensis*, under the two names in the synonymy above. Nevertheless, the fine radial external ornament of *G. homevalensis* has not been shown to be present on any Western Australian specimens. Hence, the present author considers it is reasonable to compare the somewhat variable Mingenew specimens with the well known Aktastinian, Western Australian species *Gilledia woolagensis* Campbell (1965: 82, pl. 9, figs 42, 47).

REFERENCES

References are supplementary to those in Parts 1–12 (*Proceedings of the Royal Society of Victoria*, vol. 91: 181; vol. 93: 109; vol. 95: 237; vol. 96: 83; vol. 97: 19; vol. 98: 97; vol. 99: 19; vol. 100: 21; vol. 102: 21; vol. 102: 1; vol. 103: 55; vol. 105: 1, vol. 107: 95).

ANGIOLINI, L., 1995. Permian brachiopods from Karakorum (Pakistan). Pt 1 (with appendix). *Rivista Italiana di Paleontologia e Stratigrafia* 101: 165–214.

ARCHBOLD, N. W., 1987. Studies on Western Australian Permian brachiopods 7. The strophalosiid genera *Wyndhamia* Booker, 1929, *Lialosia* Muir-Wood and Cooper, 1960 and *Liveringia* gen. nov. *Proceedings of the Royal Society of Victoria* 99: 19–35.

ARCHBOLD, N. W., 1995a. Ufimian (early Late Permian) brachiopods from the Perth Basin, Western Australia. *Memoir of the Association of Australasian Palaeontologists* 18: 153–163.

ARCHBOLD, N. W., 1995b. Studies on Western Australian brachiopods 12. Additions to the Late Asselian-Tastubian faunas. *Proceedings of the Royal Society of Victoria* 107: 95–112.

ARCHBOLD, N. W. & GAETANI, M., 1993. Early Permian Brachiopoda and Mollusca from the northwest Himalaya, India. *Rivista Italiana di Paleontologia e Stratigrafia* 99: 27–56.

ARMSTRONG, J., 1970. Syringothyrid brachiopods from the Permian of eastern Australia. *Neues Jahrbuch fur Geologie u Paläontologie, Abhandlungen* 136: 135–165.

CAMPBELL, K. S. W., 1965. Australian Permian terebratuloids. Bureau of Mineral Resources, Geology and Geophysics, Bulletin 68: 1–147.

Fig. 11. A–K, M, *Hoskingia nobilis* Etheridge, 1907a. A, B, CPC 33900, internal mould of shell in dorsal and profile views, ×1. C, I, K, CPC 33901, internal mould of shell in dorsal, profile and ventral views, ×1. D, J, GSWA F230, internal mould of shell in dorsal and ventral views, ×1.25. E–G, CPC 33902, internal mould of shell in dorsal, ventral and profile views, ×1.2. H, GSWA F49472, latex cast from external mould of dorsal valve, ×1. M, GSWA F49473, internal mould of mature shell in dorsal view, ×1. L, N–R, *Gilledia* cf. *woolagensis* Campbell, 1965. L, CPC 33903, internal mould of shell in dorsal view, ×1.4. N, CPC 33904, internal mould of shell in profile view, ×1.4. O–R, CPC 33905, internal mould of shell in dorsal, ventral, profile and anterior views, ×1.4.
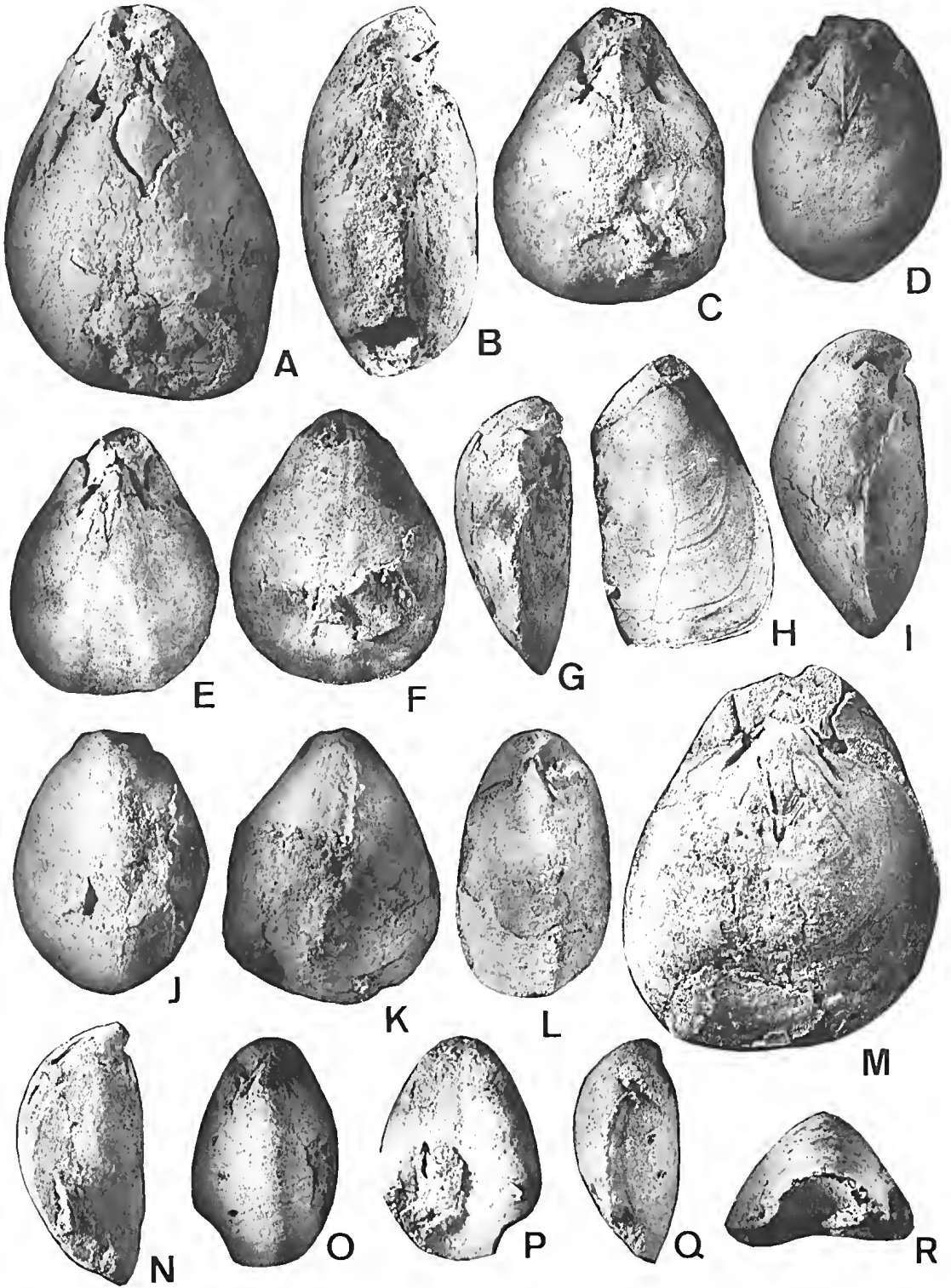
CAMPBELL, W. D., 1910. The Irwin River Coalfield, and the adjacent districts from Arrino to Northhampton. *Geological Survey of Western Australia, Bulletin,* 38: 1–108.

CLARKE, E. de C., PRENDERGAST, K. L., TEICHERT, C. & FAIRBRIDGE, R. W., 1951. Permian succession and structure in the northern part of the Irwin Basin, Western Australia. *Journal of the Royal Society of Western Australia* 35: 31–84.

DICKINS, J. M., 1956a. Fossils from Eradu and Mingenew, Western Australia. *Bureau of Mineral Resources, Geology and Geophysics, Record* 1956/19, 2 pp. (unpublished).

DICKINS, J. M., 1965. Permian fossils from the Beagle Ridge Bores BMR 10 and 10A. *Bureau of Mineral Resources, Geology and Geophysics, Report* 80: 36.

ETHERIDGE, R., Jr, 1907a. Fossils from Mingenew, Irwin River Coalfield, Western Australia, collected by Mr E. S. Simpson, Mineralogist and Assayer. *Geological Survey of Western Australia, Bulletin,* 27: 19–25, 49–56.

ETHERIDGE, R., Jr, 1915. Western Australian Carboniferous fossils, chiefly from Mount Marmion, Lennard River, West Kimberley. *Geological Survey of Western Australia, Bulletin* 58: 1–59.

GLAUERT, L., 1910. A list of Western Australian fossils (systematically arranged). *Geological Survey of Western Australia, Bulletin* 36: 71–106.

GRIGOR'EVA, A. D., KALASHNIKOV, N. V. & GIZATULIN, Z. Z., 1989. Likhareviidy Permi Timano–Pechorskoi Provintsii i ikh stratigraficheskoe Znechenic. *Trudy Institute Geologii Komi Nauchnogo Tsentra, Ural'skoe Otdelenie, Akademiya Nauk SSSR,* Vypusk 71: 26–38.

GRIGOR'EVA, A. D. & KOTLYAR, G. V., 1966. O podsemeistve Licharewiinac (Brachiopoda). *Paleontologicheskii Zhurnal* 1966 (3): 42–52.

GRUNT, T. A., 1993. Novye spirifcridy (Brachiopoda) iz nizhnei Permi Yugo-vostochnogo Pamira. *Paleontologicheskii Zhurnal* 1993 (4): 125–130.

HARRIS, L. B., 1994. Structural and tectonic synthesis for the Perth Basin, Western Australia. *Journal of Petroleum Geology* 17: 129–156.

HOSKING, L. F. V. 1933a. Fossils from the Wooramel District, Series Two. *Journal of the Royal Society of Western Australia* 19: 43–66.

LE BLANC SMITH, G. & MORY, A. J., 1995. Geology and Permian coal resources of the Irwin Terrace, Perth Basin Western Australia. *Geological Survey of Western Australia, Report* 44: 1–60.

MAITLAND, A. G., 1904. Irwin River Coalfield. *Western Australia, Annual Progress report of the Geological Survey for the year 1903:* 17–21.

MAITLAND, A. G., 1912. Relics of the Permo-Carboniferous ice age in Western Australia. *Journal of the Natural History & Science Society of Western Australia* 4: 12–29.

MAITLAND, A. G., 1919. A summary of the Geology of Western Australia. *Geological Survey of Western Australia, Memoir* 1: 1–55.

MORY, A. J., 1995. Geology of the Mingenew–Dongara 1 : 100 000 sheet. *Geological Survey of Western Australia, Explanatory Notes,* 1 : 100 000 Geological Series, 39 pp.

MORY, A. J., & IASKY, R. P., 1994. Structural evolution of the onshore northern Perth Basin, Western Australia. In *The Sedimentary Basins of Western Australia,* P. G. & R. R. Purcell, eds, Petroleum Exploration Society of Australia (WA Branch), Perth, 781–789.

MORY, A. J. & IASKY, R. P., 1995a. Geology of the Irwin River Coalfield Area, W.A. *Western Australian Geological Survey,* 1 : 100 000 (Report 44, Plate 1).

MORY, A. J. & IASKY, R. P., 1995b. Mingenew–Dongara, W.A. *Western Australia Geological Survey,* 1 : 100 000 Geological Series.

PAVLOVA, E. E., MANANKOV, I. N., MOROZOVA, I. P., SOLOVJEVA, M. N., SUETENKO, O. D. & BOGOSLOVSKAYA, M. F., 1991. Permskie Bespozvonochnye Yuzhnoi Mongolii. *Sovmestnaya Sovetsko–Mongol'skaya Paleontolgicheskaya Ekspeditsiya, Trudy* 40: 1–173.

SKWARKO, S. K., 1993. A list of Permian fossils from the Collie, Perth, Carnarvon and Canning Basins. *Geological Survey of Western Australia, Bulletin* 136: 89–109.

SOLOMINA, R. V., 1985. Novye rod brakhiopod iz verkhnei Permi Severo-Vostoka SSSR. *Paleontologicheskii Zhurnal* 1985 (2): 117–121.

STEHLI, F. G., 1961. New tercbratuloid genera from Australia. *Journal of Paleontology* 35: 451–456.

TUPPER, N. P., PHILLIPS, S. E. & WILLIAMS, B. P. J., 1994. Advances in the understanding of Upper Permian reservoir distribution and quality, North Perth Basin. In *The Sedimentary Basins of Western Australia,* P. G. & R. R. Purcell, eds, Petroleum Exploration Society of Australia (WA Branch), Perth, 823–837.

WATERHOUSE, J. B. & SHI, G. R., 1991. Late Permian brachiopod faunules from the Marsyangdi Formation, north central Nepal, and the implications for the Permian–Triassic boundary. In *Brachiopods through Time,* D. I. MacKinnon, D. E. Lee & J. D. Campbell, eds, A. A. Balkema, Rotterdam, 381–387.

POPULATION ECOLOGY OF *BANKSIA SAXICOLA* (PROTEACEAE)

N. D. Middleton[A], P. Y. Ladiges[A] & N. J. Enright[B]

[A]School of Botany, The University of Melbourne, Parkville, Victoria 3052, Australia
[B]Department of Geography and Environmental Studies, The University of Melbourne,
Parkville, Victoria 3052, Australia.

Banksia saxicola A. S. George is a rare species with a disjunct distribution, at Wilsons
Promontory National Park and the Grampians National Park, Victoria. Phenetic classification
and ordination analyses using 13 leaf, inflorescence and infructescence characters, indicated
that population differences are present but individual plants do not exclusively group into
geographically isolated populations. Plants from Mt William (Grampians) are different from
those at Wilsons Promontory, but those from Mt Rosea (Grampians) overlap with both of
these populations. Leaf flavonoid analysis revealed minor differences between Grampians and
Wilsons Promontory populations, with the latter being intermediate between *B. integrifolia*
and Grampians *B. saxicola*.

Germination of seed extracted from 1, 2–3 and >3 year old infructescences varied from
15–35% at 50 days. Seed from Wilsons Promontory had the highest germination rate. Cold
stratification of seed only promoted germination of seed >3 years of age from Mt William.
Banksia saxicola, from Wilsons Promontory, had the highest level of serotiny, although more
seed was stored per plant at Mt William due to greater fecundity. Granivory of canopy stored
seed was highest at Wilsons Promontory.

At the Grampians, *B. saxicola* is locally common, plants are generally healthy, and
spontaneous seed release together with favourable environmental conditions, have allowed
populations to regenerate in the absence of fire. At Wilsons Promontory, however, plants
are less abundant, and with no regeneration in the last 19 years the population is aging.
For continued existence of *B. saxicola* at Wilsons Promontory, conservation management
strategies need to include burning.

BANKSIA SAXICOLA A. S. George is the only
rare species of *Banksia* found in Victoria (Gullan
et al. 1990). A conservation rating of 3RC (George
1987) is designated to *B. saxicola* because popu-
lations of the species are small, occur in National
Parks and have a total range covering more than
100 km. The species has a disjunct distribution,
being found only at the Wilsons Promontory and
Grampians (Gariwerd) National Parks (Fig. 1).
Within the Grampians, *B. saxicola* grows pre-
dominantly on rocky mountain summits as shrubs
and small trees up to 6 m in height. At Wilsons
Promontory, *B. saxicola* is found as an under-
storey tree, up to 15 m in height, in wet *Eucalyptus*
forest.

The type specimen of *B. saxicola* was collected
from Mt William, Grampians, by George (1981).
B. saxicola is distinguished from *B. integrifolia*
L. f. and *B. canei* J. H. Willis, to which it is
closely related, by absence of a lignotuber, grey-
yellow coloured inflorescences, flowering time
(January to March) and whorls of relatively large
(40–100 × 10–35 mm) and often serrate leaves
(George 1981; Thiele 1993).

The disjunct distribution, differences in habit
and habitat between geographically isolated
populations, and a general lack of knowledge of
this rare species, prompted this investigation.
The aims were to identify differences between
populations relating to genetic isolation and to
document regeneration strategies and demography
of the populations. Management practices for
conservation are suggested.

MATERIALS AND METHODS

Study sites and sampling

Three populations of *B. saxicola* were sampled
at: Mt Rosea (37°18'S,142°30'E; 680–885 m asl)
and the summit of Mt William (37°18'S,142°36'E;
1167 m asl) within the Grampians National Park,
and at Wilsons Promontory National Park (39°2'S,
146°23'E; 150–280 m asl).

At Mt William (MW), *B. saxicola* and *Euca-
lyptus baxteri* (Benth.) Maiden & Blakely ex
J. Black dominate the vegetation, forming a sub-
alpine shrubland (3.5 m). Annual rainfall for the
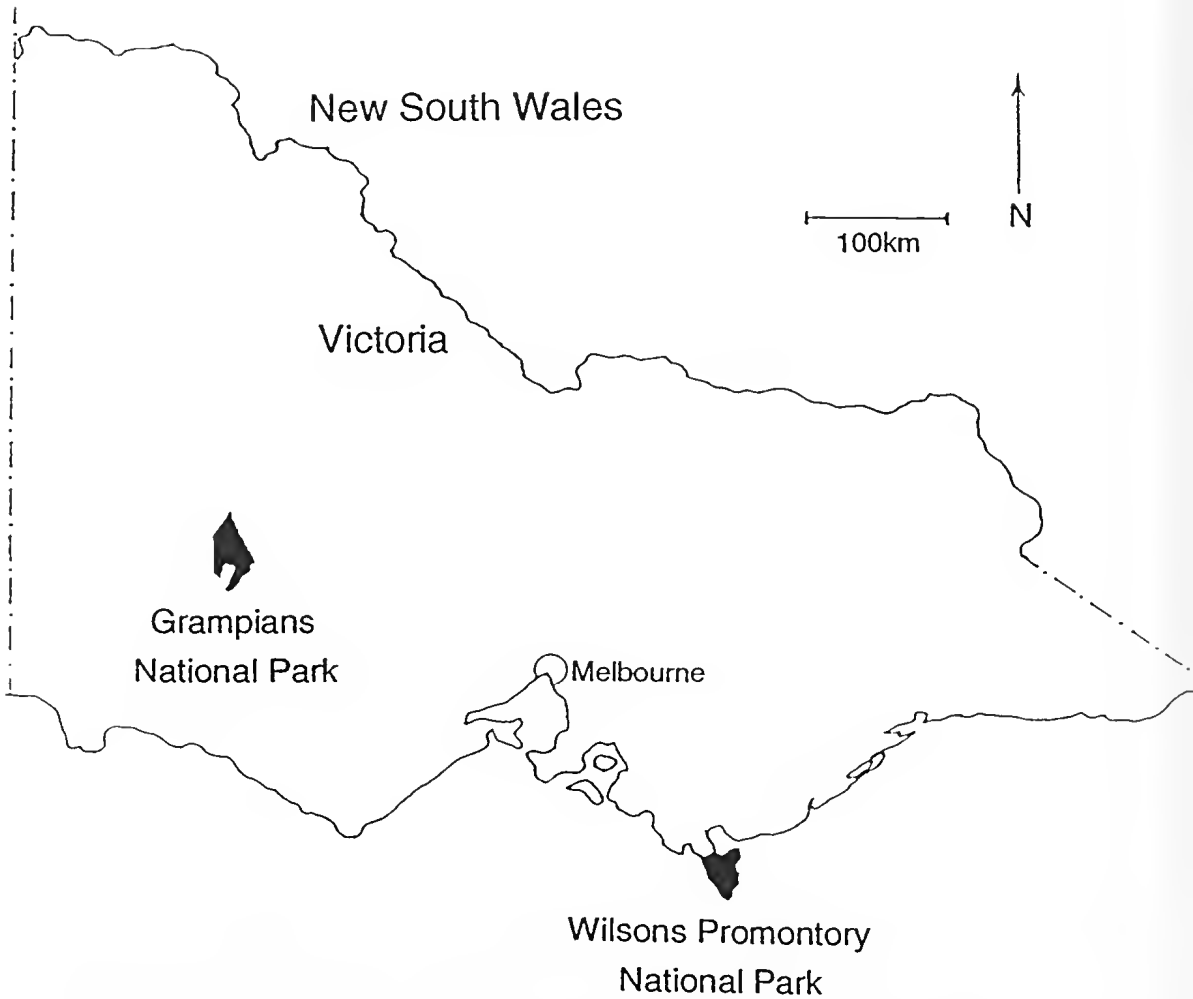
Fig. 1. Geographic distribution of National Parks within which *B. saxicola* is confined.

area averages 914 mm with snowfall occurring most years at the summit. Average daily temperatures vary from 19.9°C in summer to 8.4°C in winter. Wildfire is infrequent, last occurring in 1959. The soil is shallow and derived from medium to fine-grained quartzose sandstone. At Mt Rosea (MR) growing conditions are less severe than at MW. Snowfall is less frequent and large granite boulders provide sheltered microhabitats. Small trees and shrubs of *B. saxicola* grow up to 6.5 m in height, scattered amongst large sandstone boulders or sheltered beneath trees of *Eucalyptus serraensis* Ladiges & Whiffin. On the upper plateau of MR, fire has not occurred since 1939.

At Wilsons Promontory (WP), *B. saxicola* has a relatively restricted distribution compared with

MW and MR. Only 166 *B. saxicola* individuals were located in an area of 80 × 3000 m, 2–5 km inland, along the walking track to Sealers Cove. The area was last burnt in 1951 (T. Willett, pers. comm.). Annual rainfall averages 1051 mm, with average temperatures varying from 16.2°C in summer to 11.3°C in winter. Within this area, *B. saxicola* grows to heights of 15 m in moist gullies and on sheltered slopes. Soils are derived from granitic rocks, which are exposed throughout the area.

A population of six putative *B. saxicola* × *B. marginata* Cav. hybrids was located along Redmans Road (37°13′S,142°35′E; 490 m asl), Grampians National Park. No *B. saxicola* plants were found in this area. The sclerophyllous

woodland was dominated by *Eucalyptus obliqua* L'Hér. and *B. marginata* was abundant in the understorey.

Plants were aged by node counts (Lamont 1985) and only those plants (19–35 years old) with infructcscences (cones) were included in analyses. The number of inflorescences, sterile (barren) infructescences and 1, 2–3 and >3 year old fertile infructescences were recorded per plant. Since inflorescence buds may remain dormant for an indeterminate period of time, infructcscences were aged by colour and by degree of deterioration (Lamont 1985; Cowling et al. 1987). Where possible, six infructcscences from each age group were collected per plant. Due to the rarity of *B. saxicola*, sampling was restricted to no more than 10% of the total fruit (follicles), which in some instances led to insufficient fruit and inflorescences available for collection. Samples of leaves, including five with undamaged mucronate tips and five one year of age, were collected from each plant and used for morphological and flavonoid analyses, respectively.

Morphological analysis

Twenty-nine plants (10 MW, 12 MR and 7 WP) were scored for 13 quantitative characters (Table 1)

Leaf characters

1.	ll	leaf length
2.	lw	leaf width
3.	ll/lw	leaf length to width
4.	mtl	mucronate tip length

Inflorescence characters

5.	rl	rachis length
6.	yl	style length[A]

Fruit characters

7.	fl	follicle length
8.	fw	follicle width
9.	ufl/lfl	uppermost to lowermost follicle length

Seed characters

10.	el	endosperm length
11.	sl	seed length, including wing
12.	sw	seed width, including wing
13.	sl/el	seed to endosperm length

[A]Style length was measured at pollen presentation.

Table 1. Morphological characters used in analysis of geographic variation in *Banksia saxicola*.

for a multivariate, phenetic analysis of geographic population variation. Five measurements of each character wcre obtained and means calculated for each plant. Single factor ANOVAs and Sheffé's test were used to identify significant differences between populations for each of these characters. Plants werc compared in a multivariatc analysis using mean values of all characters and the PATN computer package (Belbin 1987). Values were range standardised and dissimilarities between plants were calculated using the metric Manhattan distance (MM). Cluster analyses were based on flexible weighted and unweighted pair-group method using averages (WPGMA and UPGMA, respectively). Ordination analyscs were performed using KYSP multidimensional scaling. KYSP was preferred to other ordination techniques because it is highly robust (Faith et al. 1987). Ordinations were viewed in the first two dimensions.

Leaf flavonoid analysis

Mature leaves wcre collected from 35 *B. saxicola* (8 MW, 11 MR and 16 WP) and 10 *B. integrifolia* subsp. *integrifolia* individuals from Wilsons Promontory. Flavonoid extraction followed that of Mabry et al. (1970). Leaves were air-dried and ground to a powder. Samples of ground leaves (2.5 g per plant) were placed in clean 25 ml glass vials with 20 ml of 80% aqueous methanol. Vials were agitated and left to settle at room temperature for 36 hours. Methanol solutions were spotted onto Whatman 3MM chromatography paper (460×570 mm) and allowed to air-dry between each of fivc applications.

Flavonoids were separated using two dimensional chromatography. An initial run using TBA (tertiary butanol:glacial acetic acid:distilled water, 3:1:1 v=v) was followed by a second, perpendicular to the first, in HOAc (15% aqueous glacial acetic acid). Chromatography papers were air-dried after each solvent application. To observe flavonoids, each dried chromatogram was viewed on a light box equipped with 360 nm Black UV fluorescent tubes. Individual flavonoids were identified by thcir position and colour prior to, and following, ammonia fume application. Since the aim was to detect any genetic variation between populations, identification of flavonoids beyond separation of compounds by colour change and chromatographic position was not necessary (T. Whiffin, pers. comm.).

Demographic analyses

Observations of ecological traits such as plant

health, death and age at reproductive maturity were noted. Age at reproductive maturity was determined by the age of trees with only one year old infructescences (i.e. plants in their first year of reproductive maturity). Because such plants totalled four, six and zero at MW, MR and WP, respectively, an additional population near Mafeking Road, Grampians National Park (37°22'S,142°34'E; 580 m asl) was included for this investigation.

For each infructescence collected (178 MW, 61 MR and 81 WP), the numbers of open and closed follicles were recorded to determine canopy seed store. Seeds were extracted by placing infructescences individually in paper bags and heating in an oven at 200°C for 5 minutes. Wet–dry cycles were occasionally required to open follicles sufficiently to remove the seed (Cowling & Lamont 1985). Once collected, seeds were categorised as firm (endosperm present and intact, presumably viable), aborted (thin, papery seed lacking endosperm) or predated (part or entire endosperm eaten by granivorous insects, leaving a pale brown granular powder; Lamont 1985; Lamont & Van Leeuwen 1988). The proportion of predated seed per infructescence was calculated and used to determine the level of granivory for infructescences of different ages within each population.

Although previous reports indicate that seed of *B. saxicola* requires a cold stratification period to break dormancy (Salkin & Hallam 1978), the altitudinal range of *B. saxicola* suggests that stratification may not be necessary for all populations. To test this, where available two samples of 10 firm seeds from each age class (1, 2–3 and >3 years) per plant were germinated. One sample was stratified at 4°C for 30 days prior to moistening, while the control sample was not treated prior to germination. For germination, seeds were placed in petri dishes on filter paper moistened with dilute Thirum fungicide (1.5 g/1000 ml distilled water). Petri dishes were placed in a growth cabinet at 15°C with a light (13 hours) and dark (9 hours) cycle, although this cycle was not expected to have any effect on germination (Sonia & Heslehurst 1978). Seeds were kept moist and germination was recorded over a 50 day period.

Statistical analysis

Mean values of the number of fertile and sterile infructescences per plant, total number of inflorescences per plant, flowers per inflorescence, follicles per infructescence, firm, aborted and predated seed per infructescence, and percentage seed germination at various time intervals, were calculated.

Percentage values for predation, serotiny and seed germination were arcsine transformed to normalise the data (Sokal & Rohlf 1987). Two-way analysis of variance (ANOVA) and Scheffé's test were used to determine the significance of differences between means ($P \leqslant 0.05$).
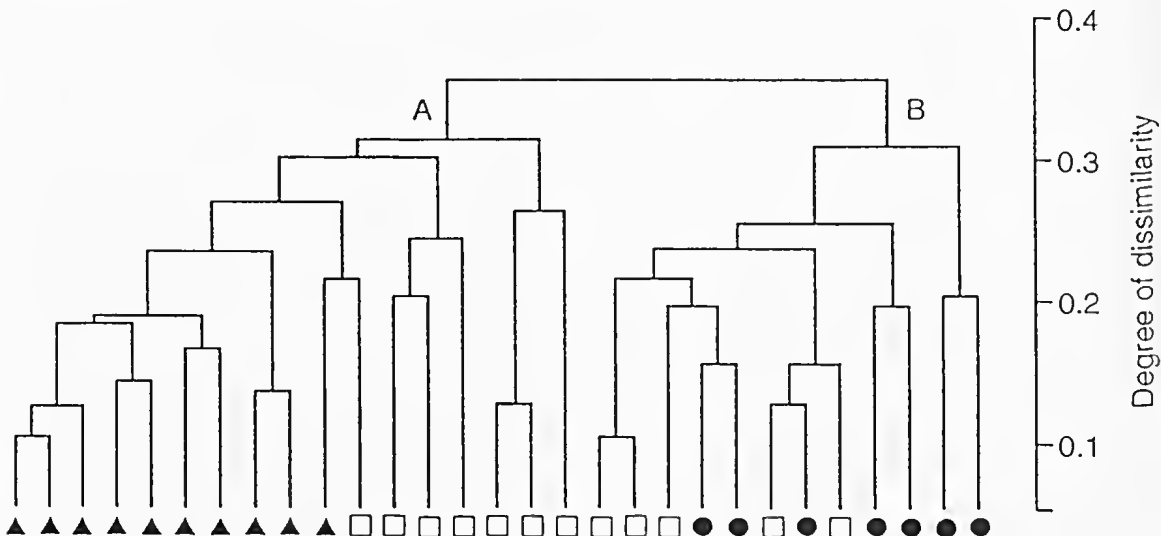
Fig. 2. Cluster analysis (MM, WPGMA) of 10 Mt William, 12 Mt Rosea and 7 Wilsons Promontory *B. saxicola* plants based on leaf, inflorescence and infructescence characters. (Black triangle = Mt William; white square = Mt Rosea; black circle = Wilsons Promontory.)

RESULTS

Morphological analysis

Cluster analyses using either WPGMA and UPGMA gave similar results, thus the WPGMA classification only is shown (Fig. 2). All MW individuals clustered into group A, all WP individuals clustered into group B, while plants from MR were more variable and were split between these two groups. The seven MR plants that clustered in group A with those from MW were collected at higher altitude than the remaining five plants from MR, which clustered in group B with plants from WP. Plants in group A had, for example, smaller leaves than plants in group B, which may be explained by plant exposure at higher altitude.

Ordination confirmed the pattern in the cluster analysis. A plot of axes 1 × 2 (Fig. 3) shows plants from WP and MW separate from one another. Seven plants from MR formed a cluster, but five overlapped in the ordination space with WP and MW. In particular, plant 16 from MR is an outlier and clustered near MW in the ordination. Plant 16 was atypical in having smaller leaves than other plants from MR.

Mean values (±standard deviation) were calculated for each morphological character for each population and one way ANOVAs and Scheffé's test indicated significance between populations for these measures (Table 2). While plants from MW have smaller leaves (ll, lw) and larger upper follicles (ufl/lfl) than those from MR and WP, plants from MW and MR have larger seeds (sw, sl, el) than those from WP.
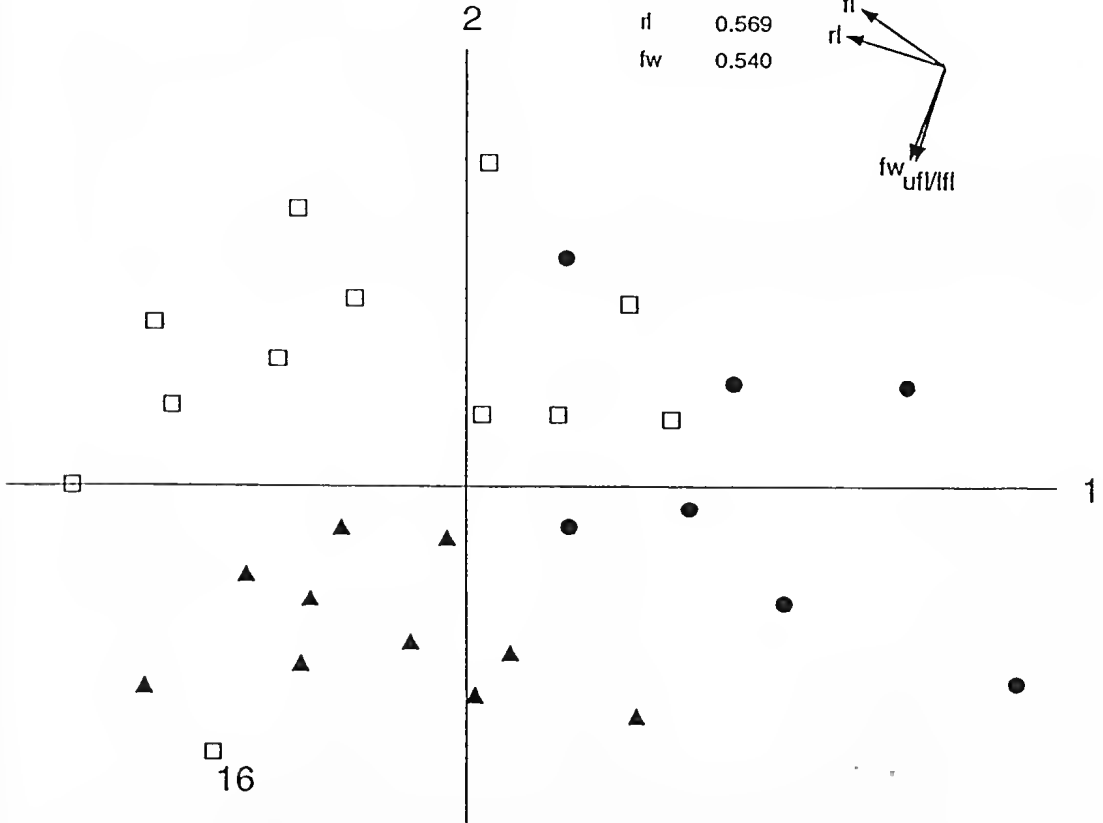
Fig. 3. Two dimensional ordination of *B. saxicola* individuals from three populations, based on morphological leaf, inflorescence and infructescence characters. (Black triangle = Mt William; white square = Mt Rosea; black circle = Wilsons Promontory; values indicate character correlation with each dimension.)

Leaf flavonoid analysis

Twenty-three leaf flavonoids were recorded for the two *Banksia* species analysed (Table 3). Flavonoid compositions of *B. saxicola* and *B. integrifolia* were very similar, with each of the 45 specimens analysed containing flavonoids 1–9. Flavonoids 10 and 11 were present in all *B. saxicola* and all but three *B. integrifolia* individuals. Variation between *B. integrifolia* and *B. saxicola* was evident by the presence of flavonoid 24. While this flavonoid was present in more than half of the *B. integrifolia* plants analysed, it was absent from all *B. saxicola* plants. Differentiation between *B. saxicola* populations was also evident. Flavonoids 22 and 23 were not observed in MW and MR populations, but were present in 88% and 38% of *B. saxicola* plants from WP, and 100% and 90% of *B. integrifolia* individuals, respectively. The higher frequency of occurrence of flavonoids 19–21 and lower occurrence of flavonoids 14–18 in *B. saxicola* from Wilsons Promontory, compared with the Grampians, indicates additional differences between these disjunct populations. Flavonoid patterns of the two Grampians populations were very similar.

Hybridisation

Observations of the roots of the six putative *B. saxicola* × *B. marginata* hybrid plants and the plants' close proximity indicate that they were probably produced by root-suckering from one individual. Infructescences of this clone had retained floral parts for some years and contained follicles that opened at maturity, similar to *B. marginata*. However, other attributes, such as arrangement, size and shape of the leaves and follicle length, indicate similarity to *B. saxicola* (Table 4).

Reproductive ecology

Although the overall germination percentage of the presumed viable seed was low (15–35%), significant differences were found between sites ($P \leqslant 0.05$). Seed collected from WP had a higher percentage germination than seed from MW and MR (Fig. 4). Contrary to a previous report (Salkin & Hallam 1978), seed of *B. saxicola* germinated without cold stratification. Overall, there was no significant difference in percentage germination between stratified and non-stratified seed when seed of different ages was pooled (Table 5a). However, when analysed according to seed age, stratification did promote germination of seed from MW that was greater than three years old ($P \leqslant 0.05$; Fig. 5). Although seed from MW showed a significant interaction effect between pre-germination treatment and seed age (Table 5b), due to lack of seed this was not tested for the other sites.

Despite the higher germination percentage of seed from WP compared to MW and MR, no recent regeneration was recorded in the field at WP. The youngest plant observed at WP was 19 years of age, the last fire being in 1951.

Character	Mt William	Mt Rosea	Wilsons Promontory	
Leaf length (mm)	56.6 ± 6.5a	78.5 ± 15.5b	86.5 ± 12.7b	***
Leaf width (mm)	21.8 ± 4.2a	23.4 ± 3.3b	28.5 ± 4.8b	**
Leaf length to width	2.7 ± 0.4a	3.5 ± 0.5ab	3.1 ± 0.5b	**
Mucronate tip length (mm)	3.3 ± 0.3	3.4 ± 1.0	2.0 ± 0.3	—[A]
Rachis length (mm)	66.9 ± 5.9	67.2 ± 12.6	58.2 ± 9.6	NS
Style length (mm)	26.5 ± 2.3	28.8 ± 1.8	27.9 ± 2.3	—[A]
Follicle length (mm)	15.1 ± 1.0	15.6 ± 1.4	14.4 ± 1.5	NS
Follicle width (mm)	5.9 ± 0.5	5.6 ± 0.6	5.4 ± 0.7	NS
Upper to lower follicle length	1.2 ± 0.1a	1.0 ± 0.1b	1.0 ± 0.1b	***
Endosperm length (mm)	9.3 ± 0.8a	9.3 ± 1.2a	7.8 ± 0.8b	**
Seed length, including wing (mm)	15.9 ± 1.2a	16.2 ± 1.8a	13.3 ± 1.3b	***
Seed width, including wing (mm)	7.4 ± 0.5a	8.2 ± 0.8a	6.3 ± 0.8b	***
Seed/endosperm length	1.7 ± 0.1	1.7 ± 0.1	1.7 ± 0.1	NS

[A] Missing data for WP rendered sample size too small for statistical comparison.

Table 2. Mean values ± standard deviation for morphological characters used in phenetic analysis. Different letters denote differences between populations at the significance level indicated (*= $P \leqslant 0.05$, **= $P \leqslant 0.01$, ***= $P \leqslant 0.001$, NS = not significant).

	Flavonoid																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
B. saxicola																								
Mt William	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+				
Grampians	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+		+		
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+				+		
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+					
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+					
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+				
Mt Rosea	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+				+		
Grampians	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+				
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+				
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+		
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+					
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+				
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+						
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+				
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+			
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+								
Wilsons	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+				+	+		+		
Promontory	+	+	+	+	+	+	+	+	+	+	+	+	+		+		+		+		+	+	+	
	+	+	+	+	+	+	+	+	+	+	+	+	+						+		+			
	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+		+		+	+		
	+	+	+	+	+	+	+	+	+	+	+	+	+	+					+	+	+	+		
	+	+	+	+	+	+	+	+	+	+	+		+	+					+	+	+			
	+	+	+	+	+	+	+	+	+	+	+	+		+	+		+	+	+	+		+		
	+	+	+	+	+	+	+	+	+	+	+	+	+		+		+	+	+		+	+		
	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+		+	+	+	+	+	+	
	+	+	+	+	+	+	+	+	+	+	+	+	+			+			+			+	+	
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+				+	
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+				+	+		+	+	
	+	+	+	+	+	+	+	+	+	+	+	+	+		+				+	+				
	+	+	+	+	+	+	+	+	+	+	+	+	+			+		+	+	+		+	+	
	+	+	+	+	+	+	+	+	+	+	+	+	+			+			+	+		+		
	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+	+	+		+		
B. integrifolia																								
subsp. *integrifolia*																								
Wilsons	+	+	+	+	+	+	+	+	+	+		+	+	+	+		+	+				+		
Promontory	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+		+	+	+	+	+	+
	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+		+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+		+	+		+		+	+
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

Table 3.   Presence of leaf flavonoids in three populations of *B. saxicola* and a single population of *B. integrifolia* subsp. *integrifolia*.

Attribute	B. marginata	Hybrid	B. saxicola
Habit[A]	shrub	tree	tree
Root-sucker	variable	most probable	unknown
Leaf length (mm)	15–60[B]	79 (66–93)[C]	40–100[B]
Leaf width (mm)	3–13[B]	13 (9–16)[C]	10–35[B]
Leaf shape	serrate towards tip oblanceolate	entire oblanceolate	entire obovate
Leaf arrangement	scattered	whorled	whorled
Serotiny level	low	low	medium
Follicle length (mm)	7–17[B]	20 (15–22)[C]	12–20[B]

[A] Although tree forms of *B. marginata* exist, only shrub forms were present in the area. In an equivalent wood-
land, *B. saxicola* forms trees.
[B] Range of values obtained from George (1981).
[C] Mean (range) from 24 samples.

Table 4. Attributes distinguishing a possible *B. saxicola* × *B. marginata* hybrid found near Redmonds Road,
Grampians National Park.
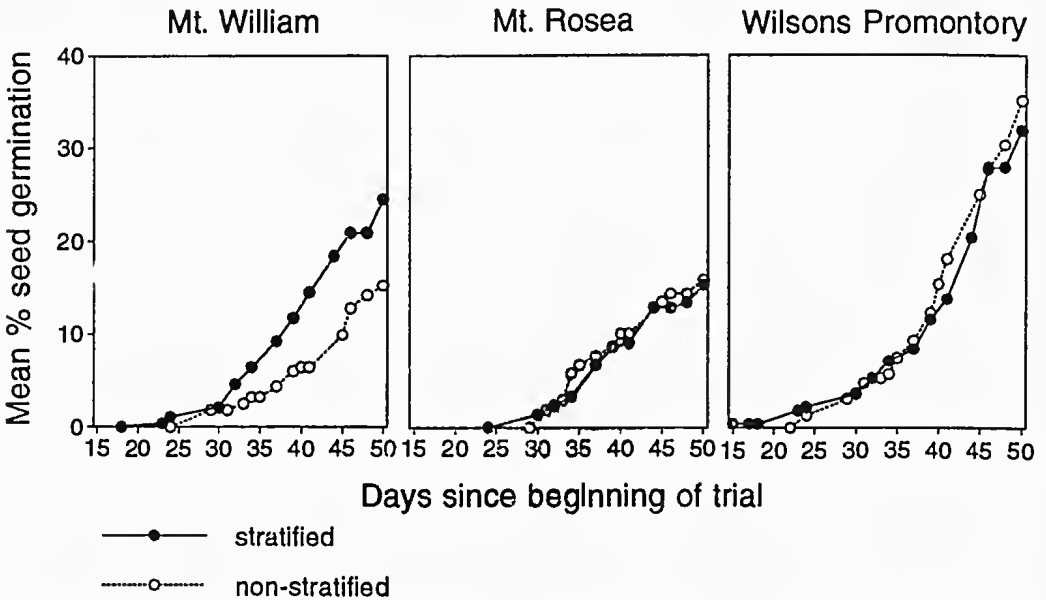
Fig. 4. Mean percentage germination over 50 days of stratified and control seed from Mt William, Mt Rosea
and Wilsons Promontory. All seeds were firm and presumed viable.

Interfire regeneration is abundant at MW and MR
and at an additional dense *B. saxicola* population
near Mafeking, Grampians. At MW, MR and
Mafeking, plants as young as 8 years of age
were producing inflorescences, however, fertile
infructescences were not seen until plants were
14–21 years of age. Data on age to reproductive
maturity could not be obtained from WP, because
all plants examined were reproductively mature
with infructescences >3 years of age. Of the
166 *B. saxicola* individuals counted at WP, 31
(16%) had fallen or were standing but lacked

foliage and were presumed dead. No dead indi-
viduals were seen at MW or MR, although at MR
many plants appeared old, with spindly prostrate
branches and low fruit production. Compared
to MR and WP, plants of an equivalent age
(>33 years) at MW were highly fecund.

Variation, both between and within populations,
was generally large for the reproductive attributes
measured (Table 6). The number of flowers per
inflorescence and follicles per infructescence did
not vary noticeably between populations. At MW
B. saxicola plants produced more inflorescences

Source	SS	df	MS	F-ratio
(a) Germination of seed from different sites and pre-germination treatments				
Treatment	79.029	1	79.029	0.255
Site	4827.479	2	2413.739	7.800 *
Treatment × Site	1020.065	2	510.032	1.648
Residual	36207.088	117	309.462	
Total	42133.661	122	3312.262	
(b) Germination of seed from MW of different ages and pregermination treatments				
Treatment	949.597	1	949.597	4.216 *
Age	538.295	2	269.147	1.195
Treatment × Age	1797.601	2	898.801	3.991 *
Residual	10811.178	48	225.233	
Total	14096.671	53	2342.778	
(c) Seed retention in infructescences of different ages and sites				
Site	617.221	2	308.611	2.596
Age	16257.006	2	8128.503	68.369***
Site × Age	1875.176	4	468.794	3.943 *
Residual	6420.106	54	118.891	
Total	25169.509	62	9024.799	
(d) Predation of seed of different ages and sites				
Site	660.906	2	330.453	4.163 *
Age	3801.322	2	1900.661	23.946***
Site × Age	1323.505	4	330.876	4.169 **
Residual	4206.673	53	79.371	
Total	9992.406	61	2641.361	

Table 5. Analysis of variance with replication using arcsine transformed data for germination, seed retention and seed predation (significance levels: *=$P \leqslant 0.05$; **=$P \leqslant 0.01$; ***=$P \leqslant 0.001$).

per year than at other sites, resulting in a greater total number of fertile (and infertile) infructescences, and therefore a greater seed store per plant than at MR and WP. The percentage of firm seeds per infructescence decreased with age of infructescence at all sites. One year old infructescences from MR contained more viable
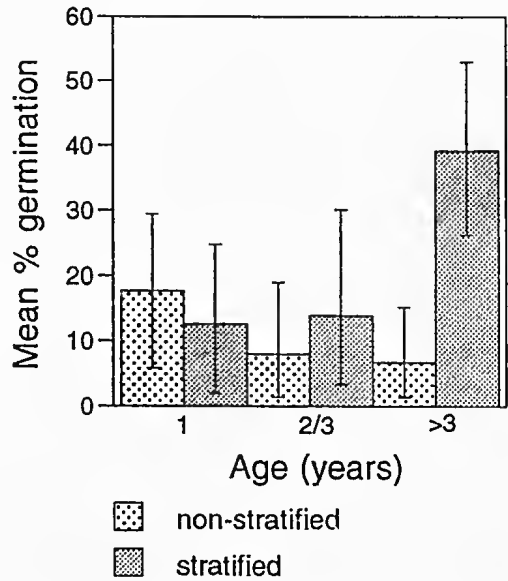
Fig. 5. Mean percentage germination of stratified and control seed of 1, 2–3 and >3 years of age from Mt William. Bars represent back-transformed upper and lower 95% confidence limits. All seeds were firm and presumed viable.

Attribute	Population		
	MW	MR	WP
Plant age (years)	(19->32)	25 (20–44)	(19->30)
Inflorescences/plant	38 (15–91)	16 (0–75)	11 (0–33)
Flowers/inflorescence	917 ±61	965 ±52	863 ±50
Fertile infructescences/plant	(28->300)	9 (1–36)	48 (10–114)
1 year fertile infructescences/plant	23 (4–75)	9 (0–13)	9 (3–16)
2–3 year fertile infructescences/plant	25 (6–75)	2 (0–8)	16 (3–50)
>3 year fertile infructescences/plant	(11->150)	5 (0–25)	16 (0–50)
Sterile infructescences/plant	(26->100)	28 (1–100)	43 (11–80)
Follicles/fertile infructescence	40±11	38±13	32±9
% aborted seed/infructescence	35±12	15±8	47±7
% firm seed/1 year infructescence	66±15	76±12	51±7
% firm seed/2–3 year infructescence	46±13	71±11	52±20
% firm seed/>3 year infructescence	30±14	33±24	25±22

Table 6. Reproductive attributes *B. saxicola* plants from Mt William, Mt Rosea and Wilsons Promontory populations. Values are presented as mean±standard deviation or mean (range). Ten, twelve and eight plants were sampled from each population respectively.

seed and fewer aborted seed than those of the same age from WP and MW. At MR the proportion of sterile infructescences was higher than at MW or WP.

An ANOVA of the percentage closed follicles per infructescence for ages 1, 2–3 or >3 years at different sites showed significant differences (Table 5c) between the three age groups (P ⩽ 0.001). The interaction factor between infructescence age and population was also significant (P ⩽ 0.05; Table 5c). The percentage closed follicles decreased more rapidly with age at MW and MR, than at WP (Fig. 6). Infructescences older than three years from MW and MR had spontaneously released 54% and 62% of their seed, respectively, while only 17% of seed had been released from plants at WP. *B. saxicola* plants from WP are therefore more serotinous than those from the Grampians.

Predation

Granivorous insects are well documented to cause reproductive losses in *Banksia* (Scott 1982; Vaughton 1990; Zammit & Hood 1986; Zammit & Westoby 1988). Larvae found in *B. saxicola* follicles were tentatively identified as *Arotrophora* (Lepidoptera: Tortricidae) or *Xyloryctis* (Lepidoptera: Xyloryctidae) using the descriptions provided by Scott (1982). *Arotrophora aucuatalis* is the most widespread predatory moth larva of *Banksia* and is capable of infecting both inflorescences and infructescences. Weevils (Curculioinidae: Coleoptera) were also found within the *B. saxicola* follicles. The level of predation varied significantly with site (P ⩽ 0.05) and age (P ⩽ 0.001). The interaction factor between site and age was also significant (P ⩽ 0.01; Table 5d). Predation of 1 year old seed was low for all sites (0.04–2.59%) and increased to the greatest level in infructescences >3 years of age collected from WP (Fig. 7).

In addition to seed loss due to insect damage, infructescences that had been attacked by birds were found on the ground at WP and MR. Loss of reproductive effort due to birds was not assessed because the plants from which infructescences originated could not be determined, however, cockatoos are known to cause heavy inflorescence and infructescence loss in some *Banksia* species (Witkowski et al. 1991).

Predation of *B. saxicola* leaves by leafminers was also observed. This was abundant at WP, less frequent at MR, and not observed at MW. Miners primarily attacked 1 year old leaves prior to February and the infected leaves were
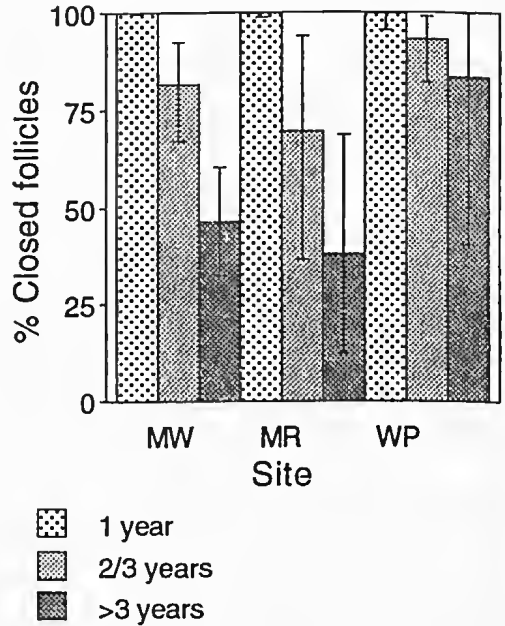
Fig. 6. Serotiny of three *B. saxicola* populations as indicated by percentage closed follicles per infructescence by infructescence age. Bars represent back-transformed upper and lower 95% confidence limits.
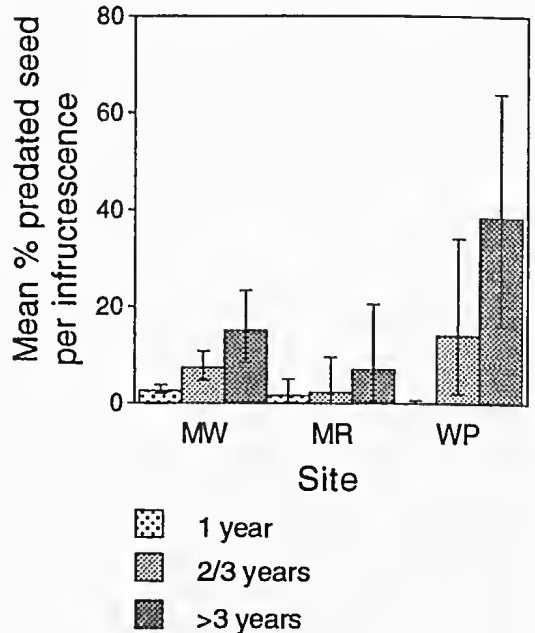
Fig. 7. Predation of *B. saxicola* seed with increase in infructescence age. Bars represent back-transformed upper and lower 95% confidence limits.

shed between March and April. Leafminers (Lepidoptera) were not identified due to their metamorphosis prior to sampling, however, the linear and blotch mines observed are comparable to mines made by Nepticulidae (Hering 1951).

DISCUSSION

Morphological analysis

Cluster analysis and ordination showed that plants from MW in the Grampians (shrub form) are different in morphology from plants from WP (tree form). However, plants from MR (Grampians) showed considerable variation, overlapping both these populations. Thus, no discrete groups correlate with the geographic disjunction of the Grampians and Wilsons Promontory (Fig. 2). Some morphological differences, such as leaf size, are probably phenotypic rather than genotypic, and hence reflect environmental differences between sites, such as altitude and exposure. In the sub-alpine environment at MW, for example, plants have the smallest leaves and the shortest stature. At MR, plants with the smallest leaves and stature were at the highest altitude and plants with the largest leaves and tallest stature were growing down slope in more sheltered habitats.

Although there is insufficient morphological disjunction within *B. saxicola* to warrant taxonomic recognition, such as Grampians and WP subspecies, the variation noted is relevant for conservation of the species' total gene pool.

Leaf flavonoid analysis

Flavonoid composition is considered stable over a wide range of environmental conditions (Leach & Whiffin 1989) and has been used as evidence of speciation, hybridisation and gene flow between plants (Mabry et al. 1970; Leach & Whiffin 1989; Whiffin & Ladiges 1992). Thiele & Ladiges (1994) identified 25 leaf flavonoids in *B. integrifolia* subsp. *integrifolia* from Victoria, whereas in the present study only 24 were found. This difference may be due to different flavonoid concentrations from different methodologies or from some flavonoids degrading over time to produce a number of breakdown products (B. Meurer-Grimes, pers. comm.). Variation in the abundance of specific flavonoids in each population, together with the absence of flavonoids 22 and 23 from MW and MR, indicate genetic differentiation between *B. saxicola* populations. Similarity in flavonoid composition between *B. saxicola* and *B. integrifolia* at WP indicates possible hybridisation between these two populations or retention of plesiomorphic (primitive) characters in *B. saxicola* at Wilsons Promontory.

Reproductive ecology

Cold stratification is a prerequisite of seed germination for many montane plants (Tran & Cavanagh 1984). In montane environments, seed release followed by immediate germination in late summer or autumn, is non-adaptive as seedlings would be vulnerable to winter frosts and snowfall. In such environments, seed dormancy is selectively preferred, delaying seed germination until spring, when conditions for seedling growth are more favourable. In montane *Banksia* species, such as *B. canei*, *B. marginata* and *B. saxicola*, a period of cold is a suggested requirement to break seed dormancy (George 1981).

A previous study on the effect of pre-germination, cold stratification on *B. saxicola*, then referred to as 'Grampians *B. integrifolia*' (Salkin & Hallam 1978) found that a minimum stratification period of 43 days at 5°C was required for seed germination. In the present study, seed was stratified for 30 days at 4°C. There was no difference in the percentage germination between nonstratified and stratified seed except for enhanced germination in seed >3 years of age collected from MW, a sub-alpine environment and the highest altitude where *B. saxicola* is found. Because of this it seems that the germination behaviour of *B. saxicola* varies with altitude, similar to *B. marginata* (Salkin & Hallam 1978). Why stratification only enhanced germination of old seed is perplexing.

Many of the reproductive traits measured for *B. saxicola* varied greatly between plants at each site. This may be due to the range in age (19–35 years) of plants included in the analysis. Although all plants were producing seed, some may have been reproductively mature for only a few years. In such cases, accumulation of fruit would be significantly lower than for plants 10 to 15 years older. Another factor that would result in variation between plants, particularly at the Grampians, is habitat variation within each site. At MW and MR, scattered boulders produce non-uniform habitats. Plants in sheltered situations between large boulders were taller and more fecund than plants in exposed situations (pers. observ.). In these rocky environments, soil depth also varies, leading to additional differences in conditions for plant growth.

Seed abortion within *Banksia* has been calculated at 22–74% depending on the species (Cowling

et al. 1987; Lamont & Barrett 1988; Lamont & van Leeuwen 1988). With 15%, 35% and 47% of seed aborted at MW, MR and WP respectively, *B. saxicola* has comparatively mid to low seed abortion rates for the genus. Lamont & Barrett (1988) suggest that seed abortion can indicate nutrient conservation by plants and may, therefore, indicate low nutrient supply. Seed abortion was lower at MR than MW or WP, however, plants at MR produced fewer fertile infructescences and a higher proportion of sterile infructescences than these two sites, therefore high nutrient supply at MR seems unlikely. Cowling et al. (1987) found that more serotinous *Banksia* species produced lower proportions of aborted seed. For *B. saxicola*, however, this relationship is not evident as plants from WP had the highest level of serotiny and the highest level of seed abortion. At MW, plants produce more inflorescences each year, resulting in a greater annual addition to the canopy seed store. The number of follicles per infructescence did not vary between localities, suggesting no difference in pollinator availability between sites.

Percentage firm seed per infructescence (an estimate of percentage viable canopy-stored seed) decreased with infructescence age due to spontaneous seed release, predation and decomposition. *B. saxicola* was found to have 66% (MW), 76% (MR) and 51% (WP) firm seed (for 1 year-old infructescences). In comparison with other species in the genus, *B. saxicola* may be considered to have medium percentage viable seed (see Cowling et al. 1987; Lamont & Barrett 1988; Lamont & van Leeuwen 1988).

Although *B. saxicola* plants may be seen flowering at eight years of age (Taylor & Hopper 1988), they do not produce viable seed until they are 14–21 years old. For the first few years of flowering only sterile infructescences are produced. This and the delay between first flower and first fruit production have been noted in other *Banksia* species (Lamont 1985; Gill & McMahon 1986; Salkin 1986; Whelan & Goldingay 1986; Lamont & Barret 1988; Witkowski et al. 1991). Reasons for this phenomenon remain unknown. Within *Banksia* flower to fruit ratios are typically low. Although not well understood, this could be due to spacial constraints, lack of nutrients, unavailability of pollinators, or mechanisms by which plants can selectively favour development of seeds produced by outcrossing (Salkin 1986; Whelan & Goldingay 1986; Fuss & Sedgley 1991).

Serotiny is well developed in Australian sclerophyllous vegetation. *B. saxicola* is often characterised as spontaneously releasing the majority of

its seed within three years of production (George 1987; Wrigley 1989). In the present study, however, rarely were infructescences found with all seeds released (<1% of infructescences collected). In *Banksia*, 76% of taxa store seed within the canopy for release when infructescences dry or are burnt (Cowling & Lamont 1985; Gill 1976). Variation in the degree of serotiny (the rate of seed release) occurs both within and between *Banksia* species (Lamont 1985). Due to the difficulty in accurately aging *B. saxicola* seed, a value for the degree of serotiny following the method of Lamont (1991), could not be calculated. A qualitative estimate obtained from Fig. 6 indicates that plants from WP, the most moist site, were more serotinous than those from the Grampians.

Predation

Several species of insect are known to reduce available seed levels in *Banksia* (Scott 1982). These may or may not be species specific predators and are capable of destroying flowers and/or seeds. Scott (1982) concluded that insects infest inflorescences, and remain in the rachis until the seeds develop, such that seed predation occurs primarily in the first year of fruit formation. In such situations, granivory should not increase with infructescence age, as was found here (Fig. 7). A number of other studies have also found a higher level of granivory in older infructescences (Cowling et al. 1987; Zammit & Westoby 1988; Witowski et al. 1991; N. Enright, unpubl. data). Despite large variation in the amount of *B. saxicola* seed predation at each site (11–39%), average values are comparable to other *Banksia* species (negligible to 40%; Zammit & Hood 1986; Zammit & Westoby 1988; Witkowski et al. 1991).

Response to fire, regeneration and conservation

The effect of fire on *B. saxicola* is poorly understood. Taylor & Hopper (1988) list 'resprouting', 'plant death with no seedling regeneration' and 'unspecified' as responses of *B. saxicola* to fire, which is relatively ambiguous. Despite this, *B. saxicola* is generally thought to be killed by fire with regeneration occurring from seed released from the canopy (George 1981; D. Cheal, pers. comm.). Evidence for this includes thin bark (2–4 mm) and the absence of a lignotuber (George 1981).

Species in which follicles open spontaneously (without fire) usually form uneven-aged stands (Lamont 1985). Such interfire regeneration is

occurring at MW and MR. At WP, despite an uneven aged population and some seed release (17%), no *B. saxicola* plants under 19 years of age were found. Factors preventing regeneration at WP remain largely untested. Seed viability does not appear to be limiting as seed from WP was found to germinate at a higher rate than MW or MR when germinated under laboratory conditions (Fig. 4). Possible reasons for lack of recruitment at WP, aside from low seed release, could include an increased incidence of post-dispersal fungal attack and unsuitable germination/growing conditions. The moister environment at the WP site would enhance decomposition and fungal attack by *Rhizoctonia* and *Pythium*, which commonly cause damping-off in cultivated *Banksia* seedlings (McLean 1993). At WP the lower level of light beneath the canopy (pers. observ.) than at MR and MW may also result in conditions unfavourable for seedling establishment. Fire is, therefore, likely to be important for the survival of *B. saxicola* at Wilsons Promontory National Park not only to release seed from the canopy but to create favourable conditions for germination and seedling growth.

To determine a suitable fire management regime for conservation of *B. saxicola* at WP, plant age at reproductive maturity, and the level and rate of seed accumulation are required (Lamont 1985). Because the latter is unknown for *B. saxicola*, the fire interval required is best (and most conservatively) estimated as two times the plant age at reproductive maturity (A. Gill, pers. comm.). This corresponds to a 30–40 year fire interval for *B. saxicola*.

The use of fire as an ecological management tool within National Parks is a multifaceted and controversial topic. Fire regime (intensity, interval and season) and the response to fire by the community (flora and fauna) are the main ecological dilemmas. As *B. saxicola* predominantly flowers in late summer and seeds are mature after one year, late summer and autumn fires would maximise seed recruitment. This is important since *B. saxicola* is thought to be killed by fire and, therefore, relies on post-fire seed recruitment for survival.

CONCLUSION

Banksia saxicola occurs as geographically and hence genetically, isolated populations in the Grampians National Park and Wilsons Promontory National Park, Victoria. Results of morphological and flavonoid analysis indicate some degree of variation between Grampians and Wilsons Promontory populations. Because these population differences appear to be phenotypic as well as genotypic and are not clear-cut, taxonomic division of *B. saxicola* is not warranted. Genetic differences between populations require further study using molecular methods. Nevertheless, the degree of intraspecific variation noted here, the rarity of the species and its disjunct pattern of distribution, are sufficient reasons for devising a conservation management plan for *B. saxicola* at both WP and the Grampians.

At the Grampians National Park, *B. saxicola* is locally common and regeneration is occurring in the absence of fire. Fire management proposals include burning of communities containing *B. saxicola* at intervals of 20–30 years for rocky woodlands and >40 years for sub-alpine communities (Anon. 1985). Under these regimes continued existence of *B. saxicola* is likely to be assured.

At Wilsons Promontory, *B. saxicola* is less abundant than at the Grampians. No regeneration has occurred for 19 years and the population is at risk of extinction. Although a considerable quantity of relatively viable seed is retained within the canopy of this aging population, predation of seed is high and has been shown to increase with seed age. Because only 17% of seed is released spontaneously in the Wilsons Promontory population, a fire is required to release the bulk of seed and produce optimum conditions for germination (increase light incidence, decreased competiton, etc.). Burning only part of the *B. saxicola* stand at WP and growing plants from seed away from the site for transplanting would act as a safeguard, in case conditions for post-fire recruitment are sub-optimal.

A small area along the walking track to Sealers Cove at WP has been set aside as a Scientific Protection Area where off-track access is prohibited, primarily to protect *B. saxicola* (Anon. 1987). The species occurs both within and outside of this area. Within this zone, public use, safety and education are highly prioritised management objectives, therefore, the use of fire in ecological management is limited. Because the population of *B. saxicola* at WP has not been burnt since the 1951 wildfire (42 years ago), a burn in the near future is strongly advised.

using PATN, and the Department of Conservation and Natural Resources for permission to study and collect plant material from Wilsons Promontory and Grampians National Parks.

REFERENCES

ANON., 1985. *Grampians National Park Plan of Management*, National Parks Service, Melbourne.

ANON., 1987. *Wilsons Promontory National Park Management Plan*, National Parks Service, Melbourne.

BELBIN, L., 1987. PATN. *Pattern Analysis Package Reference Manual*, CSIRO, Division of Wildlife and Rangelands Research, Canberra.

COWLING, R. M. & LAMONT, B. B., 1985. Seed release in *Banksia*: the role of wet–dry cycles. *Australian Journal of Ecology* 10: 169–171.

COWLING, R. M., LAMONT, B. B. & PIERCE, S. M., 1987. Seed bank dynamics of four co-occurring *Banksia* species. *Journal of Ecology* 75: 289–302.

FAITH, D. P., MINCHIN, P. R. & BELBIN, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69: 57–68.

FUSS, A. M. & SEDGLEY, M., 1991. Pollen tube growth and seed set of *Banksia coccinea* R. Br. (Proteaceae). *Annals of Botany* 68: 377–384.

GEORGE, A. S., 1981. The genus *Banksia* L. f. (Proteaceae). *Nuytsia* 3: 239–473.

GEORGE, A. S., 1987. *The Banksia Book*, Kangaroo Press, Kenthurst.

GILL, A. M., 1976. Fire and the opening of *Banksia ornata* F. Muell. follicles. *Australian Journal of Botany* 24: 329–335.

GILL, A. M. & MCMAHON, A., 1986. A post-fire chronosequence of cone, follicle and seed production in *Banksia ornata*. *Australian Journal of Botany* 34: 425–433.

GULLAN, P. K., CHEAL, D. C. & WALSH, N. G., 1990. *Rare or Threatened Plants in Victoria*, Department of Conservation and Environment: Victoria.

HERING, E. M., 1951. *Biology of Leaf Miners*, W. Junk, Gravenhage.

LAMONT, B. B., 1985. Fire responses of sclerophyll shrublands: A population ecology approach, with particular reference to the genus *Banksia*. In *Symposium on Fire Ecology and Management in Western Australian Ecosystems*, J. R. Ford, ed., W.A. Institute of Technology, Perth, pp. 41–46.

LAMONT, B. B., 1991. Canopy seed storage and release — what's in a name? *Oikos* 60: 266–268.

LAMONT, B. B. & BARRETT, G. J., 1988. Constraints on seed production and storage in a root-suckering *Banksia*. *Journal of Ecology* 76: 1069–1082.

LAMONT, B. B. & VAN LEEUWEN, S. J., 1988. Seed production and mortality in a rare *Banksia* species. *Journal of Applied Ecology* 25: 551–559.

LEACH, G. J. & WHIFFIN, T. 1989. Ontogenetic, seasonal and diurnal variation in leaf volatile oils and leaf phenolics of *Angophora costata*. *Australian Systematic Botany* 2: 99–111.

MABRY, T. J., MARKHAM, K. R. & THOMAS, M. B., 1970. *The Systematic Identification of Flavonoids*, Springer-Verlag, New York, pp. 3–7.

MCLEAN, R., 1993. *Banksia* propagation. *Society for Growing Australian Plants Newsletter* 60: 6–8.

SCOTT, J. K., 1982. The impact of destructive insects on reproduction in six species of *Banksia* L. f. (Proteaceae). *Australian Journal of Zoology* 30: 901–921.

SALKIN, A., 1986. Breeding systems in eastern Australian banksias. *Victorian Naturalist* 103: 43–47.

SALKIN, A. & HALLAM, N. D., 1978. The topodemes of *Banksia canei* J. H. Willis (Proteaceae). *Australian Journal of Botany* 26: 707–721.

SOKAL, R. R. & ROHLF, F. J., 1987. *Introduction to Biostatistics*, 2nd edn, Freeman and Company, New York.

SONIA, L. & HESLEHURST, M. R., 1978. Germination characteristics of some *Banksia* species. *Australian Journal of Ecology* 3: 179–186.

TAYLOR, A. & HOPPER, S., 1988. *The Banksia Atlas*. Australian Flora and Fauna Series No. 8, Canberra Publishing and Printing Company, Canberra, pp. 216–217.

THIELE, K. R., 1993. A Cladistic Analysis of *Banksia* L. f. Ph. D. Thesis. School of Botany, The University of Melbourne.

THIELE, K. R. & LADIGES, P. Y., 1994. The *Banksia integrifolia* L. f. species complex (Proteaceae). *Australian Systematic Botany* 7: 393–408.

TRAN, V. N. & CAVANAGH, A. K., 1984. Structural aspects of dormancy. In *Seed Physiology, Germination and Reserve Metabolization*, Vol. 2, D. R. Murray, ed., Academic Press, Australia, pp. 1–40.

VAUGHTON, G., 1990. Predation by insects limits seed production in *Banksia spinulosa* var. *neoanglica* (Proteaceae). *Australian Journal of Botany* 38: 335–340.

WHELAN, R. J. & GOLDINOAY, R. L. 1986. Do pollinators influence seed-set in *Banksia paludosa* Sm. and *Banksia spinulosa* R. Br.? *Australian Journal of Ecology* 11: 181–186.

WHIFFIN, T. & LADIGES, P. Y., 1992. Patterns of variation and relationships in the *Eucalyptus alpina-E. baxteri* complex (Myrtaceae) based on leaf volatile oils. *Australian Systematic Botany* 5: 695–709.

WITKOWSKI, E. T. F., LAMONT, B. B. & CONNELL, S. J., 1991. Seed bank dynamics of three co-occurring banksias in south coastal Western Australia: the role of plant age, cockatoos, senescence and interfire establishment. *Australian Journal of Botany* 39: 385–397.

WRIGLEY, J. W., 1989. 'Banksias, Waratahs and Grevilleas and all other plants in the Australia Proteaceae family.' Collins Publishers, Australia.

ZAMMIT, C. & HOOD, C. W., 1986. Impact of flower and seed predators on seed-set in two *Banksia* shrubs. *Australian Journal of Ecology* 11: 187–193.

ZAMMIT, C. & WESTOBY, M., 1988. Pre-dispersal seed losses, and the survival of seeds and seedlings of two serotinous *Banksia* shrubs in burnt and unburnt heath. *Journal of Ecology* 76: 200–214.

HALACARIDAE (ACARI) FROM THE GREAT BARRIER REEF. DESCRIPTION OF A NEW SPECIES OF *COPIDOGNATHUS*

ILSE BARTSCH

Biologische Anstalt Helgoland, Notkestr. 31, 22607 Hamburg, Germany

Copidognathus glandulifer sp. nov. is described. The species is closely related to *C. curassaviensis* Viets, recorded from the Caribbean area, but differs from the latter in that the porose panels of the dorsal plates are larger, the costae of the posterodorsal plate are curved posteriorly, and the spur of telofemur 1 is shorter. Both species belong to the *curassaviensis* species group.

NUMEROUS studies deal with marine macro- and meiofauna of the Great Barrier Reef (Cameron et al. 1974; Choat et al. 1988), but marine mites are not recorded. This paper presents a description of a halacarid species that belongs to the *curassaviensis* species group of the genus *Copidognathus*.

METHODS

The mites were cleared in lactic acid and mounted in glycerine jelly. Drawings were prepared using a camera lucida. The holotype is lodged in the Museum of Victoria (MV), other material in the MV and the author's halacarid collection.

Abbreviations used in the description: AD, anterior dorsal plate; AE, anterior epimeral plate; ds, dorsal seta(e) of idiosoma; ds-1 to ds-6, first to sixth pair(s) of dorsal setae; GA, genitoanal plate; GO, genital opening; OC, ocular plate(s); P, palp; P-2 to P-4, second to fourth palpal segment(s); PD, posterior dorsal plate.

Genus Copidognathus Trouessart, 1888

Copidognathus glandulifer sp. nov.

Figs 1, 2

Type material. Holotype female: MV K-3762, from Mac Gillivray Reef, NE of Lizard Island, 14°39'S, 145°29'E, 2 m depth, coarse sand, March 1994, coll. C. Erséus.

One female: MV K-3763, from Lizard Island (ca 240 km N of Cairns), north end of Second Beach, 14°40'S,145°26.5'E, 1 m depth, coarse sand and gravel, March 1994, coll. C. Erséus.

One female: author's collection, from Heron Reef, off Gladstone, at the Bommi SW of Heron Island, 12 m depth, heterogeneous fine to medium sand, April 1994, coll. C. Erséus.

Diagnosis

Female. Idiosomal length 360–384 μm. Raised areolae of dorsal plates with porose panelled areolae. AD with pair of large lateral and two small median porose areolae; OC with two elongate areolae; PD with pair of longitudinal, posteriorly curved costae and small lateral areolae. PD with single pair of large glands. Palps slender, only slightly surpassing the stout rostrum. Leg I larger than succeeding legs. Ventral seta of telofemur I spur-like. Tibia I ventrally with a slender and two spur-like setae. Claws on tarsi II–IV with delicate pectines.

Description

Idiosoma 360–384 μm long, 198–217 μm wide, holotype 378 μm long. Dorsal plates (Fig. 1A) with raised, porose areolae, remainder of plate reticulate, with large polygons which in turn are reticulate (Fig. 1D). Porose areolae with panels, each with five to ten canaliculi. Intense eye pigment beneath AD and OC. AD 125 μm long, 101 μm wide, almost hexagonal in outline, its anterior margin slightly protruding. AD with two distinctly raised and two small, only slightly raised porose areolae; one of two last-mentioned areolae anterior to median distinctly raised areola, the other near posterior margin of the plate. Gland pores large; first pair in lateral angles of pair of porose areolae. OC 105 μm long, 62 μm wide; anterior cornea distinctly larger than posterior one. Gland pores lateral to posterior cornea. OC with two elongate porose areolae, one medial to corneae, the other one along lateral margin of OC. PD 196 μm long, 149 μm wide. Pair of medial longitudinal costae in posterior portion of PD curved and bending anteriad; left costa thus J-shaped, right costa
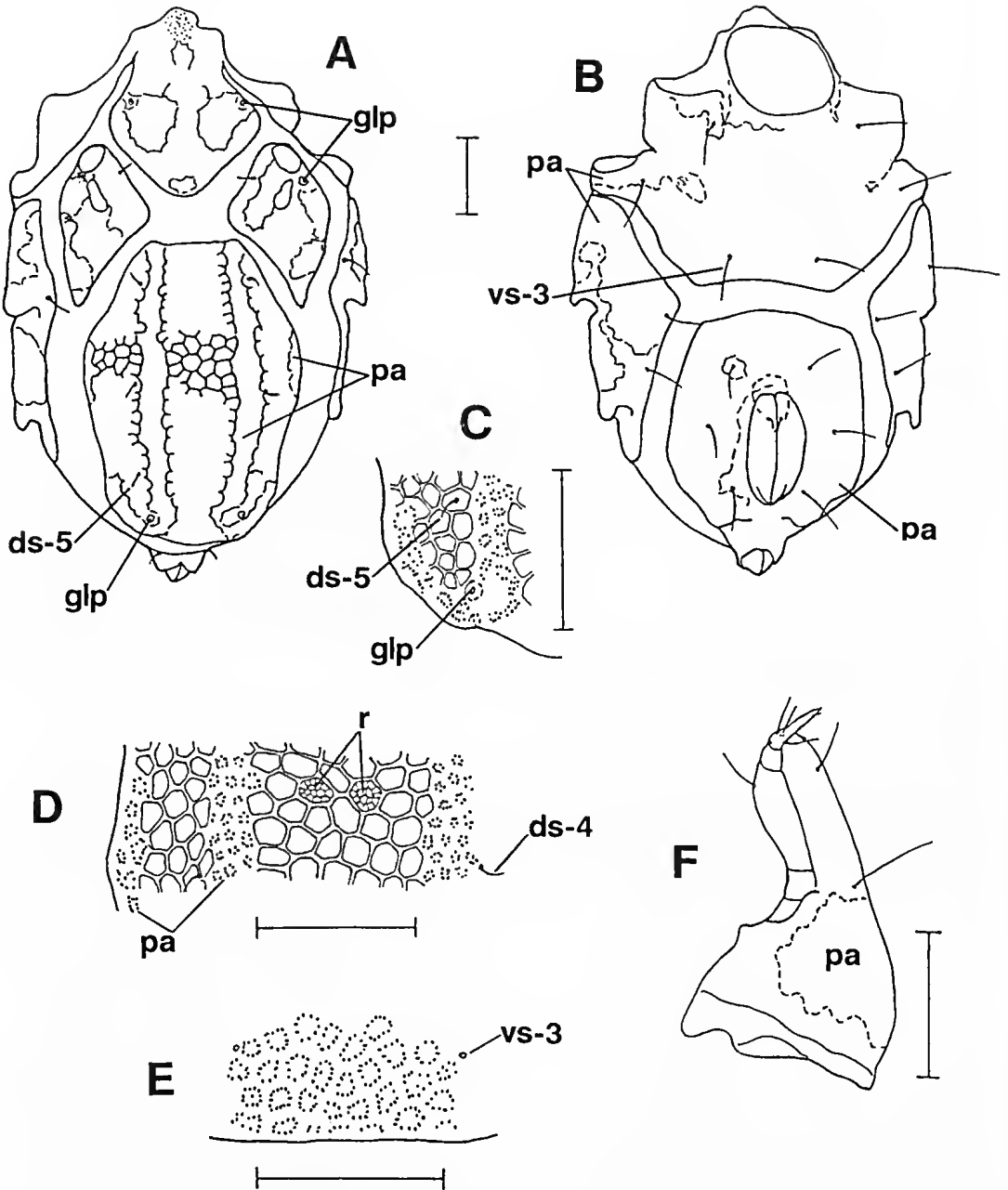
Fig. 1. A–F, *Copidognathus glandulifer* sp. nov., female. A, idiosoma, dorsal. B, idiosoma, ventral (right half with broken lines indicating borders of porose areolae). C, posterior portion of left PD. D, portion of median and left PD level with ds-4 (with two of the polygons showing the reticulation). E, posterior portion of AE level with vs-3. F, gnathosoma, lateral. Bar scale = 50 μm. (ds-4, ds-5, fourth and fifth dorsal seta; glp, gland pore; pa, porose areola; r, reticulation; vs-3, third pair of ventral setae.)
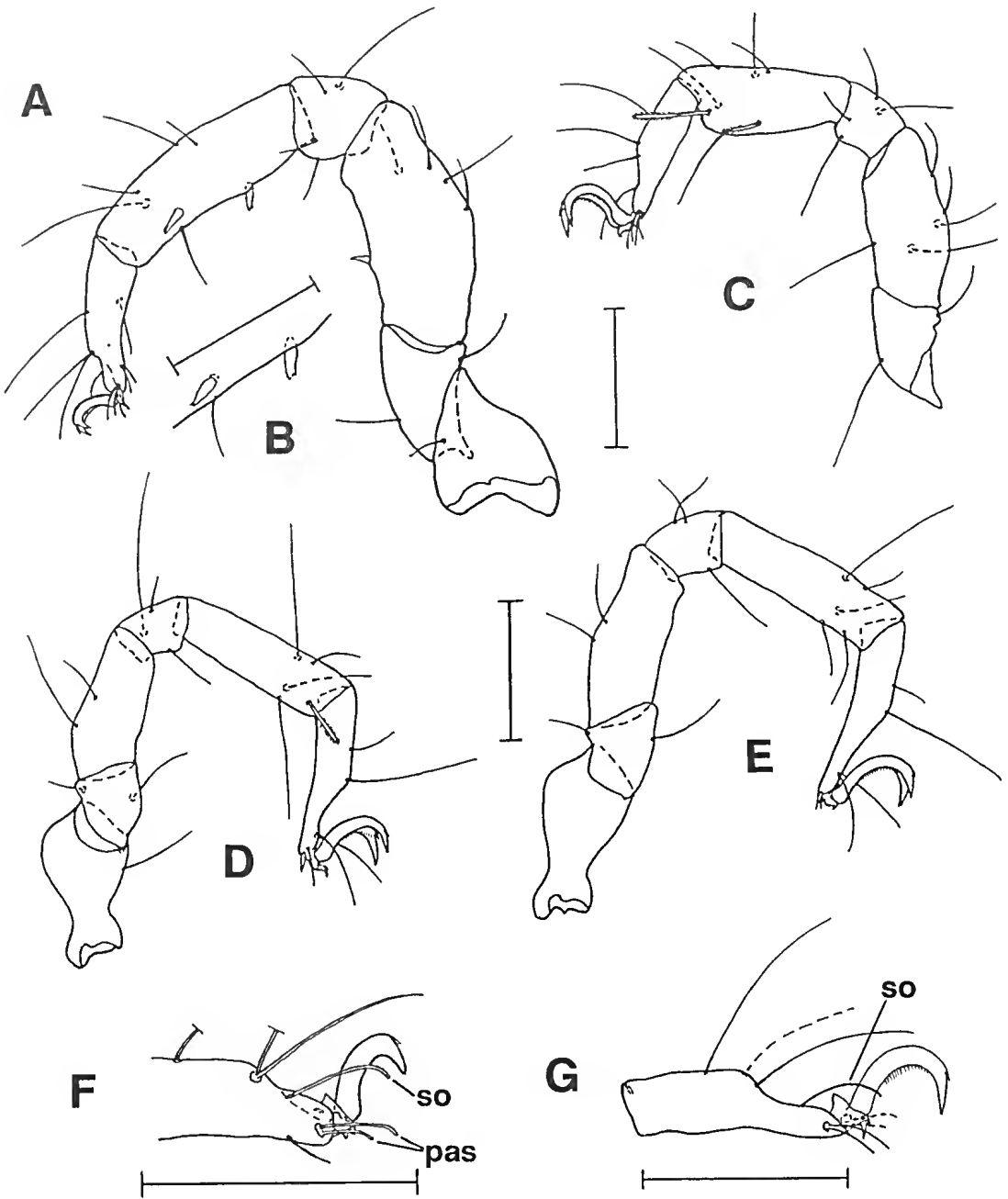
Fig. 2. A–G, *Copidognathus glandulifer* sp. nov., female. A, leg I, medial. B, ventral portion of tibia I, medial. C, telofemur-tarsus II, medial. D, leg III, medial. E, leg IV, medial. F, tip of tarsus I, lateral (ventral seta and the medial eupathid and the doubled parambulacral setae omitted). G, tarsus II, lateral (distomedial seta and medial parambulacral setae in broken lines). Bar scale = 50 μm. (pas, parambulacral setae; so, solenidion.)

mirror-inverted. Costae mostly three porose panels wide. Short lateral costae one to two porose panels wide. A single pair of enlarged gland pores in posterior portion of PD (Fig. 1C). Setae ds-1 on AD, inserted near medial edge of pair of porose areolae. Setae ds-2 in anteromedial margin of OC. Setae ds-3, ds-4 and ds-5 in lateral margin of medial porose costae, ds-3 and ds-4 anterior and posterior to a level with insertion of leg III respectively, ds-5 posterior to a level with insertion of leg IV. Setae ds-6 on anal cone.

Most of ventral plates coarsely porose; canaliculi generally arranged along margins of polygons (Fig. 1E). AE 107 μm long, 230 μm wide (Fig. 1B). GA 179 μm long, 135 μm wide. GO large, 72 μm long, 41 μm wide; distance from anterior margin of GA to that of GO less than length of GO. Genital sclerites with pair of subgenital setae. Perigenital setae arranged as illustrated. Ovipositor extending beyond GO for 11 μm.

Gnathosoma (Fig. 1F) 132 μm long. Rostrum stout, shorter than gnathosomal base. Palps very slender, P-2, P-3 and P-4 41, 7 and 25 μm long. Palps only slightly extending beyond rostrum.

Leg I larger than the other legs (Fig. 2A). Leg I, as well as leg II, with telofemora and tibiae subequal in length; legs III and IV with their tibiae being longer than telofemora. Tibia I almost cylindrical, telofemur I widened, 2.4 times longer than high. Number of setae, from trochanter to tibia: leg I, 1, 2, 5, 4, 7; leg II, 1, 2, 5, 4, 7; leg III, 1, 2, 2, 3, 5; leg IV, 0, 2, 2, 3, 5. Ventral seta of telofemur I very short and spur-like. Tibia I with two bluntly ending spurs and a short, seta-like bristle (Fig. 2B). Tibia II (Fig. 2C) with a slender ventral and two bipectinate ventromedial bristles; distal bristle larger than proximal one. Tibia III (Fig. 2D) with a coarsely bipectinate and a long, smooth bristle. Both ventral bristles on tibiae IV (Fig. 2E) smooth and slender. Tarsus I (Fig. 2F) with three dorsal setae and a 20 μm long dorsolateral solenidion, a long ventral seta, a pair of ventral eupathid setae and a pair of doubled parambulacral setae. Membranes of claw fossa present though reduced. Tarsus II (Fig. 2G) dorsally with three setae; basal seta conspicuously slender; distolateral seta stouter than distomedial one. Parambulacral setae doubled. Tarsi III and IV each with four dorsal setae; basal one shorter than the other setae. Tip of tarsus III with slender medial and spur-like lateral parambulacral seta. Both parambulacral setae on tarsus IV spur-like.

Paired claws on tarsus I much smaller than those of the other legs. Claws with accessory process. Pectines of claws on tarsi II–IV provided with very delicate tines. Median claw on tarsus I bidentate, both dents similar in size. Median claw on the other legs with reduced dorsal dent.

Remarks

The most conspicuous external characters are: porose areolae of dorsal plates panelled, each panel with five (on PD) to ten (on AD) canaliculi; AD with four porose areolae, OC with two elongate areolae, PD with pair of longitudinal, posteriorly curved costae, and pair of short lateral areolae; gland pores enlarged; PD with single pair of gland pores; ventral plates coarsely porose; palps slender, only slightly extending beyond rostrum; telofemur I with ventral spur; tibia I with two bluntly-ending spur-like bristles; genua I–IV each with four, four, three and three setae.

Copidognathus glandulifer is closely related to *C. curassaviensis* Viets, 1936, a species recorded from the Caribbean area (Viets 1936). Differences between *C. glandulifer* and *C. curassaviensis* are: the AD has larger porose areolae and the porose areolae of the OC are more elongate in *C. glandulifer* than in *C. curassaviensis*, the costae on the PD of *C. glandulifer* are J-shaped, and the spur on telofemur I is shorter than in *C. curassaviensis*.

In general facies, *Copidognathus glandulifer* is very similar to *C. elaboratus* Bartsch, 1996, a species recorded from Northern Australia (Bartsch 1996). The outline of the idiosoma, the dorsal and ventral plates and also the outline of the porose areolae are similar in both species; both species have enlarged gland pores; leg I is longer than the other legs and tibia I has two short, bluntly ending spines; the palps are slender and short, just extending to the end of the rostrum. Differences are in the shape of the pores within the porose areolae, the number of glands, the outline of the palps and the number of setae on genu IV. The porose areolae of *C. elaboratus* bear deep ostia from rosette pores, the canaliculi do not pierce the surface of the integument, in contrast, *C. glandulifer* has porose panels, each with five to ten canaliculi, ostia are lacking. The PD of *C. elaboratus* has two pairs of glands, the PD of *C. glandulifer* a single pair. The palps of *C. elaboratus* have spine-like ventral lamellae whereas the palps of *C. glandulifer* are cylindrical. Genu IV of *C. elaboratus* bears four setae, that of *C. glandulifer* three setae.

DISCUSSION

The cosmopolitan genus *Copidognathus* contains almost 300 species. Diagnostic features are, e.g.,

size, outline and ornamentation of the idiosoma and its plates, the gnathosoma and legs, presence and outline of the porose areolae, and number, arrangement and size of the setae, glands and gland pores. About 25 species are characterized by the combination of, conspicuous glands and enlarged gland pores; intensely sclerotized plates with raised porose areolae on the dorsal plates and coarsely porose ventral plates; an anteriorly protruding AD and its pair of porose areolae being circular or ovate in form but not fused; small and inconspicuous epimeral processes; short ovipositor; clavate trochanters III and IV without spine-like dorsomedial lamellae; two dorsal but no ventral setae on telofemora III and IV. The idiosoma of these species is about 1.3–1.7 times longer than wide, never remarkably slender. The majority of these species belong to the *bairdi* group. Apart from the characters mentioned above, species of the *bairdi* group have two pairs of glands on the PD and the genua IV bear four setae. Species placed into the *bairdi* group are: *C. acanthoscelus* Bartsch, 1992a, *C. africanus* Bartsch, 1972, *C. bairdi* Newell, 1947, *C. bairdiensis* Bartsch, 1984, *C. elaboratus* Bartsch, 1996, *C. euryalus* Bartsch, 1996, *C. frontispinus* Bartsch, 1972, *C. gibberipes* Viets, 1936, *C. gitae* Chatterjee, 1991, *C. glandulosus* Bartsch, 1984, *C. grandiculus* Bartsch, 1977, *C. hawaiiensis* Bartsch, 1989, *C. malaysius* Bartsch, 1993, *C. monacanthus* Bartsch, 1992a, *C. obesus* Bartsch, 1984, *C. ornatus* Bartsch, 1981, *C. sidellus* Bartsch, 1985, *C. sideus* Bartsch, 1982, *C. spinula* (Trouessart, 1899), *C. temaeus* Bartsch, 1992b, *C. umbonatus* Bartsch, 1992a, and *C. unispinosus* Bartsch, 1989. *C. ganglionatus* Newell, 1984, *C. triareolatus* Newell, 1984 and *C. tuberans* Newell, 1984, assumedly also belong to the *bairdi* group but the descriptions of some details are inadequate or contradictory. The *bairdi* group in turn can be subdivided (Bartsch 1996).

The two species *C. curassaviensis* and *C. glandulifer*, at a first glance resembling representatives of the *bairdi* group, belong to the *curassaviensis* group, named after *Copidognathus curassaviensis* Viets. Characters of the *curassaviensis* group are: dorsal plates with porose panels; gland pores enlarged; PD with single pair of gland pores; ventral plates with coarse porosity; ovipositor only slightly extending beyond GO; tibia 1 with two bluntly ending spurs; genu IV with three setae; telofemora III and IV with two setae each; palps slender and short, hardly extending beyond stout rostrum. The most obvious differences to representatives of the *bairdi* group are, the PD of species of the *curassaviensis* group has

a single pair of enlarged gland pores and genu IV three setae.

The majority of the species of the *bairdi* group live in warm temperate and tropical waters all around the globe. Similarly, representatives of the *curassaviensis* group are thought to inhabit shallow tropical waters of all oceans. Beside *C. curassaviensis* which was taken in a tidal sand pool on the shores of Curaçao (Viets 1936) and *C. glandulifer* from the Great Barrier Reef another species of this group was found in sandy deposits of Mactan Island, Philippines (unpublished record).

ACKNOWLEDGEMENTS

REFERENCES

BARTSCH, I., 1972. Halacaridae (Acari) aus Südafrika. *Mitteilungen aus dem hamburgischen Zoologischen Museum und Institut* 69: 5–32.

BARTSCH, I., 1977. Interstitielle Fauna von Galapagos. XX. Halacaridae (Acari). *Mikrofauna des Meeresbodens* 65: 1–107.

BARTSCH, I., 1981. Halacaridae (Acari) aus dem Kanal von Moçambique. *Cahiers de Biologie marine* 22: 35–63.

BARTSCH, I., 1982. Weitere Halacaridae (Acari) aus dem Kanal von Moçambique. *Cahiers de Biologie marine* 23: 435–457.

BARTSCH, I., 1984. New species of the *bairdi* group in the genus *Copidognathus* (Acari, Halacaridae). *Bulletin of marine Science* 35: 200–210.

BARTSCH, I., 1985. Zur Halacaridenfauna (Halacaridae, Acari) der Philippen. Beschreibung von drei neuen Arten. *Mitteilungen aus dem hamburgischen Zoologischen Museum und Institut* 82: 269–277.

BARTSCH, I., 1989. New species of *Copidognathus* (Acari: Halacaridae) from Hawaiian Islands. *Occasional Papers of the Bernice P. Bishop Museum* 29: 138–148.

BARTSCH, I., 1992a. Halacaridae (Acari) from Hong Kong. Three new species of *Copidognathus*. *Entomologische Mitteilungen aus dem Zoologischen Museum, Hamburg* 10: 229–241.

BARTSCH, I., 1992b. Halacariden von der Insel Moorea und Bora Bora, Gesellschaftsinseln, Polynesien (Arachnida: Acari). *Senckenbergiana biologicae* 72: 465–488.

BARTSCH, I., 1993. Halacaridae (Acari) von Malaysia. Beschreibung von drei Arten der Gattung *Copidognathus*. *Entomologische Mitteilungen aus dem Zoologischen Museum, Hamburg* 11: 45–58.

BARTSCH, I., 1996. Copidognathinae (Halacaridae, Acari) from Northern Australia. Description of four species. In *Proceedings of the Sixth International Marine Biological Workshop: The Marine Flora and Fauna of Darwin Harbour, Northern Territory, Australia*, R. Hanley, ed.

CAMERON, A. M., CAMPBELL, B. M., CRIBB, A. B., ENDEAN, R., JELL, J. S., JONES, O. A., MATHER, P. & TALBOT, F. J., 1974. *Proceedings of the Second International Symposium on Coral Reefs*. Vol. 1. The Great Barrier Reef Committee, Brisbane, 630 pp.

CHATTERJEE, T. 1991. *Copidognathus gitae*, a new species of Halacaridae (Acari) from Visakhapatnam coast, Bay of Bengal. *Journal of the Bombay Natural History Society* 88: 272–275.

CHOAT, J. H., BARNES, D., BOROWITZKA, M. A., COLL, J. C., DAVIES, P. J., FLOOD, P., HATCHER, B. G., HOPLEY, D., HUTCHINGS, P. A., KINSEY, D., ORME, G. R., PICHON, M., SALE, P. F., SAMMARCO, P., WALLACE, C. C., WILKINSON, C., WOLANSKI, E. & BELLWOOD, O., 1988. *Proceedings of the Sixth International Coral Reef Symposium, Townsville, Australia*. Vols I–III. The 6th International Reef Symposium Executive Committee, Townsville, 285 pp., 867 pp., 867 pp.

NEWELL, I. M., 1947. A systematic and ecological study of the Halacaridae of eastern North America. *Bulletin of the Bingham Oceanographic Collection* 10: 1–232.

NEWELL, I. M., 1984. Antarctic Halacaroidea. *Antarctic Research Series* 40: 1–284.

TROUESSART, E. L., 1888. Note sur les Acariens marins recueillis par M. Giard au laboratoire maritime de Wimereux. *Compte rendu de l'Académie des Sciences, Paris* 107: 753–755.

TROUESSART, E. L., 1899. Description d'espèces nouvelles d'Halacaridae. *Bulletin de la Société d'études scientifiques d'Angers* 29: 209–223.

VIETS, K., 1936. Zoologische Ergebnisse einer Reise nach Bonaire, Curaçao und Aruba im Jahre 1930. No. 18. Halacariden aus Westindien. *Zoologische Jahrbücher, Systematik* 67: 389–424.

PERMIAN FOSSIL MARINE INVERTEBRATES FROM THE NORTHERN TERRITORY DESCRIBED BY ROBERT ETHERIDGE JUNIOR

N. W. Archbold[A], R. H. Swart[A] & J. M. Dickins[B]

[A] School of Aquatic Science and Natural Resources Management, Deakin University,
Rusden Campus, 662 Blackburn Road, Clayton, Victoria 3168
[B] Australian Geological Survey Organisation, GPO Box 378, Canberra, ACT 2601

Archbold, N. W., Swart, R. H. & Dickins, J. M., 1996:12:31. Permian fossil marine invertebrates from the Northern Territory described by Robert Etheridge Junior. *Proceedings of the Royal Society of Victoria* 108(2): 63–71. ISSN 0035-9211.

Three specimens of Permian marine fossil invertebrates, previously thought to be possibly lost but now known to be housed in the collections of the Museum of Victoria, are photographically illustrated for the first time and taxonomically reassessed. Lectotypes are formally selected for *Oriocrassatella stokesi* Etheridge fil. and *Bellerophon pennatus* Etheridge fil. The palaeobiogeography of *Oriocrassatella* is briefly reviewed.

ROBERT ETHERIDGE Junior described numerous Permian marine invertebrate fossils from the region of Treachery Bay, Port Keats area, Northern Territory, in a series of four reports published from 1895 to 1907. Many of the specimens that were originally collected by the Government Geologist of South Australia, Henry Yorke Lyell Brown, and his staff are housed in the South Australian Museum and several of these have been refigured (Dickins 1963; Archbold 1981, 1986; Archbold & Thomas 1993). However a few important specimens were not located in the South Australian Museum (Dickins 1963: 103, 186); currently they are housed in the Museum of Victoria.

The Museum of Victoria obtained the specimens when it purchased in 1972 the fossil collections of the Kyancutta Museum (South Australia). It appears likely that the Kyancutta Museum obtained the material from the Port Adelaide Institute Museum which received material donated by H. Y. L. Brown (Dr T. A. Darragh, Museum of Victoria personal communication to N.W.A.). The present work photographically illustrates the specimens from the Museum of Victoria for the first time and designates lectotypes for the species *Oriocrassatella stokesi* Etheridge fil. and *Bellerophon pennatus* Etheridge fil. The missing ventral valve internal mould of *Megasteges septentrionalis* (Etheridge fil.), reported by Archbold (1986), is re-illustrated and discussed briefly.

STRATIGRAPHY, LOCALITIES AND AGE

The onshore Permian stratigraphy of the Port Keats District, Bonaparte Basin, Northern Territory has been documented by Thomas (1957, 1958) and Dickins et al. (1972) and summarised by Skwarko (1993a). Faunal horizons within the onshore sequence were progressively elucidated by Thomas (1957), Dickins et al. (1972) and Archbold (1988). A relatively informal series of stratigraphical names was developed for the onshore Permian sequence as compared with a formal named sequence of units for offshore sequences (see tables 4 and 5 in Skwarko 1993a). Table 1 summarises the onshore terminology of various authors and the current understanding of faunal horizons in the Port Keats District compared with both the Australian Geological Survey Timescale (see Archbold & Dickins 1996) and the brachiopod zonation scheme for the Permian of Western Australia (Archbold 1993, 1995).

Material illustrated and discussed herein comes from two faunal horizons within the Port Keats sequence. *Oriocrassatella stokesi* and *Bellerophon pennatus* were collected from the marine beds which crop out at Fossil Head. These beds share numerous brachiopod species with the fauna of the Coolkilya Sandstone of the Carnarvon Basin and the Lightjack Formation of the Canning Basin (Archbold 1993). The Faunas of these units are considered to belong to the Middle to Late Kungurian *Neochonetes (Sommeriella) afanasyevae* Zone, a view consistent with earlier studies of the bivalves (Dickins 1956). The specimen of *Megasteges septentrionalis*, which could not be located for the revision of the species (Archbold 1986), came from Cape Dombey, from beds high in the 'Upper Marine Beds' of Thomas (1957) considered to be Dzhulfian in age (previously referred to the Chhidruan, see Archbold 1988) and belonging to the *Waagenoconcha (Winnonoconcha) imperfecta* Zone.

DEVELOPMENT OF ONSHORE STRATIGRAPHY AND BIOSTRATIGRAPHY, BONAPARTE BASIN

BRACHIOPOD ZONES ARCHBOLD, 1988, 1993

- *Waagenoconcha (Wiman.) imperfecta*
- *Liveringia magnifica*
- *Neochonetes (Sommeriella) afanasyevae*
- *Wyndhamia colemani*

DICKINS et al., 1972

- Upper Marine Beds
- Plant bearing Sandstones
- Beds at Fossil Head
- Locality 627 Beds
- Keep Inlet Beds

THOMAS, 1957

PORT KEATS GROUP

- Upper Marine Beds — Assemblage D — Assemblage C
- Plant bearing Sandstones — Assemblage B — *Glossopteris* etc.
- Lower Marine Beds — Assemblage A.

ETHERIDGE, 1907

- Cape Ford and Cape Dombey Beds
- Fossil Head Sandstones

WESTERN AUSTRALIA BRACHIOPOD ZONATION

- *Waagenoconcha (Wiman.) imperfecta*
- *Liveringia magnifica*
- *Sulciplica occidentalis*
- *Fusiplicifer coolkilyaensis*
- *Neochonetes (Sommeriella) afanasyevae*
- *Svalbardia thomasi*
- *Neo. (S.) nalbiaensis*
- *F. wandageensis*
- *Fusiplicifer cundlegoensis*
- *Tornquistia magna*
- *Fusiplicifer byroensis*
- *Wyndhamia colemani*
- *Echinalosia prideri*
- *Strophalosia jimbaensis*
- *Neo. (S.) sp. nov. A*
- *Strophalosia irwinensis*
- *Trigonotreta occidentalis*
- *Lyonia lyoni*

STAGES

- DORASHAMIAN = CHANGHSINGIAN
- DZHULFIAN
- MIDIAN
- KAZANIAN
- UFIMIAN
- KUNGURIAN
- ARTINSKIAN — BAIGENDZHINIAN, AKTAST.
- STERLIT.
- TASTUBIAN
- SAKMARIAN
- ASSELIAN

SERIES

- TATARIAN
- LATE PERMIAN
- EARLY PERMIAN

Table 1. Development of stratigraphy of onshore Permian sequence of the Port Keats District, Northern Territory and brachiopod zones currently recognised within the sequence.

PALAEOBIOGEOGRAPHY
OF *ORIOCRASSATELLA*

The occurrence of crassatellid bivalves in Late Palaeozoic strata was first documented in detail in a beautifully illustrated account by Yakovlev (1902) that has often been overlooked by subsequent workers. Yakovlev studied a range of specimens, from numerous localities within the Kazanian of the Russian platform, referred to the species described by Golovkinskiy (1868: 368, pl. 3, figs 21–23) as *Schizodus planus*. Golovkinskiy's lithographic illustrations do not accurately show the dentition of the species but Yakovlev's photographic illustrations (1902, pl. 10, figs 1–7) provide clear details of the exterior of the species and the dentition of both valves. Yakovlev (1928) subsequently designated Golovkinskiy's species as the type species of *Procrassatella*. In 1902 he referred *Schizodus planus* to the Cretaceous genus *Crassatellina* Meek. Etheridge (1907) independently recognised the occurrence of crassatellid bivalves in the Late Palaeozoic sequence at Fossil Head, Northern Territory, and named the new genus *Oriocrassatella*, with type species *O. Stokesi*.

Since the pioneer studies reviewed above, numerous reports of *Procrassatella* and *Oriocrassatella* have been made around the globe. *Procrassatella* was considered to be a junior subjective synonym of *Oriocrassatella* by Newell (1958), a view anticipated by Teichert (1951: 82), and this has been accepted by subsequent authors.

The geologically oldest record of *Oriocrassatella* is that of *O. compressa* Maxwell (1964) from the Namurian of the Barrington District, New South Wales (Campbell & McKelvey 1972). *O. compressa* was originally described from localities attributed to the Late Carboniferous and Early Permian Rands and Burnett Formations of the Yarrol Region, Queensland (Maxwell, 1964). However after reassessment of the localities by one of us (J.M.D.) they are considered to be of comparable age to the New South Wales occurrences.

Numerous records of *Oriocrassatella* from throughout Gondwanaland and peripheral regions are known from the Sakmarian and Early Artinskian. South American records include those from Argentina (Gonzalez 1976, 1982; Mancenido et al. 1976). Australian records are from the Bowen Basin of Queensland (Dickins 1961) and the Perth, Carnarvon and Canning Basins of Western Australia (Dickins 1963; Dickins & Skwarko 1993). Late Sakmarian–Aktastinian records of the genus are also known from the Badhaura Formation, Rajasthan, Peninsula India (Dickins & Shah 1979). Kashmir (Reed 1932), Northwest Xizang (Liu & Cui 1983), Afghanistan (Termier et al. 1974) and Oman (Dickins & Shah 1979).

Baigendzhinian records of the genus are those from the Coyrie Formation and Mallens Sandstone of the Carnarvon Basin, Western Australia (Dickins 1963; Dickins & Skwarko 1993) and the Aimau Formation, Irian Jaya (Dickins & Skwarko 1981). A Brazilian record appears to be of Baigendzhinian age (Rocha Campos 1970; Dickins 1993: 528).

Kungurian records of *Oriocrassatella* are those of the type species, *O. stokesi*, from the Nalbia and Coolkilya Sandstones of the Carnarvon Basin, the Lightjack Formation of the Canning Basin and the beds at Fossil Head, Bonaparte Basin, and an apparently closely related species from the Munurudshakskiy Horizon of Prikolymia and the upper Magiveemskoi Suite of the Omolon Massif, Northeastern Siberia. The latter species was described and figured as *Astartella omolonica* by Muromtseva (1984: 87, pl. 38, figs 12–16).

The Late Ufimian and Kazanian were apparently times of radiation of the genus into the Northern Hemisphere with species in Greenland (Newell 1955), Spitzbergen (Boyd & Newell 1977), Arctic Russia including the Taimyr Peninsula, the Verkhoyansk Mountains, Kanin Peninsula, the Pechora Basin and the Pay-Khoya (Muromtseva 1984; Kanev 1994), the Russian platform (Golovkinskiy 1868; Yakovlev 1902) and western Primor'ya (Lobanova 1961). North American occurrences are restricted to two localities in Wyoming and one in Utah (Boyd & Newell 1968, 1977). Southern Hemisphere Late Ufimian–Kazanian occurrences appear to be restricted to the faunizone 10 of Tasmania (Clarke & Farmer 1976: 107; Clarke 1987: 262).

Reports of *Oriocrassatella* younger than the Kazanian are less well documented but include reports from the Dzhulfian of Basleo and correlative localities in Timor (Hamlet 1928; Wanner 1940) and the Cherrabun Member of the Hardman Formation, Canning Basin, Western Australia (Dickins et al. 1989; Skwarko 1993b). From personal observation (J.M.D.) an undescribed species occurs in the Wairaki Breccia, Southland, New Zealand, of possible Djhulfian age. A report of small *Oriocrassatella* (as *Procrassatella*) specimens from the Kaliningrad region Russia (eastern Zechstein Basin) by Suveizdas (1975: 145, pl. 30, figs 22, 23) is of considerable interest in view of the apparent absence of the genus in the western part of the Zechstein sea (Logan 1967).

The current knowledge of the distribution in space and time of *Oriocrassatella* may indicate

a complex history of migration through time, shifting from a Southern Hemisphere origin in the Carboniferous to a broad global distribution in the Late Permian. Nevertheless the genus appears to have avoided, during its evolution and migrations, the coldest waters of the Gondwanaland region. *Oriocrassatella* appears to have been restricted in its habitat to sub-littoral elastic deposits.

SYSTEMATIC PALAEONTOLOGY

Phylum MOLLUSCA

Class BIVALVIA

Superfamily CRASSATELLACEA Ferussae, 1822

Family CRASSATELLIDAE Ferussae, 1822

Subfamily ORIOCRASSATELLINAE Boyd and Newell, 1968

Genus **Oriocrassatella** Etheridge, 1907

Type species. *Oriocrassatella Stokesi* Etheridge, 1907, from the Kungurian beds at Fossil Head, Port Keats District, Bonaparte Basin, Northern Territory.

Subjective junior synonym. *Procrassatella* Yakovlev, 1928; type species *Schizodus planus* Golovkinskiy, 1868, from the Kazanian of the Russian Platform.

Comments. *Oriocrassatella stokesi* has been described by a number of authors (Etheridge 1907; Prendergast 1935; Dickins 1956, 1963; Newell 1958; Dickins & Skwarko 1993) and is known from the Nalbia and Coolkilya Sandstones of the Carnarvon Basin, the Lightjaek Formation of the Canning Basin and the beds at Fossil Head, Bonaparte Basin. Maxwell (1964: 12) indicated, in error, that the type specimens came from the Nalbia and Coolkilya Sandstones of the Carnarvon Basin. All occurrences of the species are considered to be Kungurian in age (Archbold & Dickins 1996).

Oriocrassatella stokesi Etheridge, 1907

Fig. 1A, B, I

Edmondia, or *Chaenomya*—Etheridge 1895: 33.
Edmondia—Etheridge 1897: 15, pl. 1, fig. 10.

Oriocrassatella Stokesii—Etheridge 1906: 41 (*nomen nudum*).
Oriocrassatella Stokesi—Etheridge 1907: 9, pl. 6, figs 2–5.
cf. *Protoschizodus*—Chapman 1924a: 36.
Oriocrassatella stokesi—Eth. fil., Chapman 1924b: 7.
Protoschizodus c.f.—Chapman 1924c: 19.
Oriocrassatella stokesi—Etheridge Jnr, Prendergast 1935: 25, pl. 2, figs 19, 20.
Oriocrassatella—Teichert 1941: 383.
Oriocrassatella stokesi—Teichert 1952: 117, 129, 130.
Oriocrassatella stokesi—Etheridge Jnr, Thomas & Dickins 1954: 221.
Oriocrassatella—Condon 1954: 85, 86, 87, 92, 94, 95.
Oriocrassatella stokesi—Etheridge Jnr, Dickins 1956: 33, pl. 6, figs 8–14.
Oriocrassatella—Teichert 1957: 68.
Oriocrassatella stokesi Eth., Thomas 1957: 180.
Oriocrassatella stokesi—Etheridge Jnr, Newell 1958: 3, fig. 2.
Oriocrassatella stokesi—Etheridge fil., Dickins *in* Guppy et al. 1958: 53.
Oriocrassatella stokcsi Eth., Thomas 1958: 2.
Oriocrassatella stokesi—Etheridge Jnr, Dickins 1963: 186, pl. 18, figs 6–15.
Oriocrassatella stokesi—Etheridge Jnr, Condon 1967: 173, 184.
Oriocrassatella stokesi—Playford et al 1975: 288.
Oriocrassatella stokesi—Etheridge Jnr, Dickins & Skwarko 1993, microfiche supplement, p. 40, pl. 48, figs 15–17.

Lectotype. Herein selected. The right valve figured by Etheridge (1907, pl. 6, figs 2, 3), housed in the collections of the Museum of Victoria (registered number NMV P30707) and refigured herein in Fig. 1A, B and 1. The second specimen figured by Etheridge (1907, pl. 6 figs 4, 5) and Dickins (1963, pl. 18, fig. 7) becomes the paralectotype. Dickins (1963, pl. 18, fig. 8) also figured a plaster replica of the hinge region of what is now the lectotype.

Comments. The lectotype is the best preserved right valve yet known from the type locality. We note that the posterdorsal profile is concave unlike the convex profile of *O. elongata* Boyd & Newell (1968: 41) and the straight or gently concave posterdorsal profile of *O. plana* Golovkinskiy, see Yakovlev (1902, pl. 10, figs 1, 4–7) and Boyd & Newell (1977, figs A, B, E, G–I). We also note that the anterior cardinal tooth of the lectotype is poorly developed and hence differs subtlely from the well developed teeth of Late Permian species.

Fig. 1. A, B, D–I all from beds at Fossil Head, Treachery Bay, Port Keats Area, Bonaparte Basin, Northern Territory. C from beds at Cape Dombey, Port Keats Area, Bonaparte Basin, Northern Territory. A, B, I, *Oriocrassatella stokesi* Etheridge fil., 1907, lectotype, NMV P30707, natural cast of a right valve in interior and exterior views, ×1, and hinge interior ×2.2. D–H, *Bellerophon pennatus* Etheridge fil., lectotype, NMV P30031, natural cast of shell in anterior, adapertural, posterior adapertural, side and apertural views, ×1. C, *Megastegcs septentrionalis* Etheridge fil., NMV P30708, ventral valve internal mould, ×1.
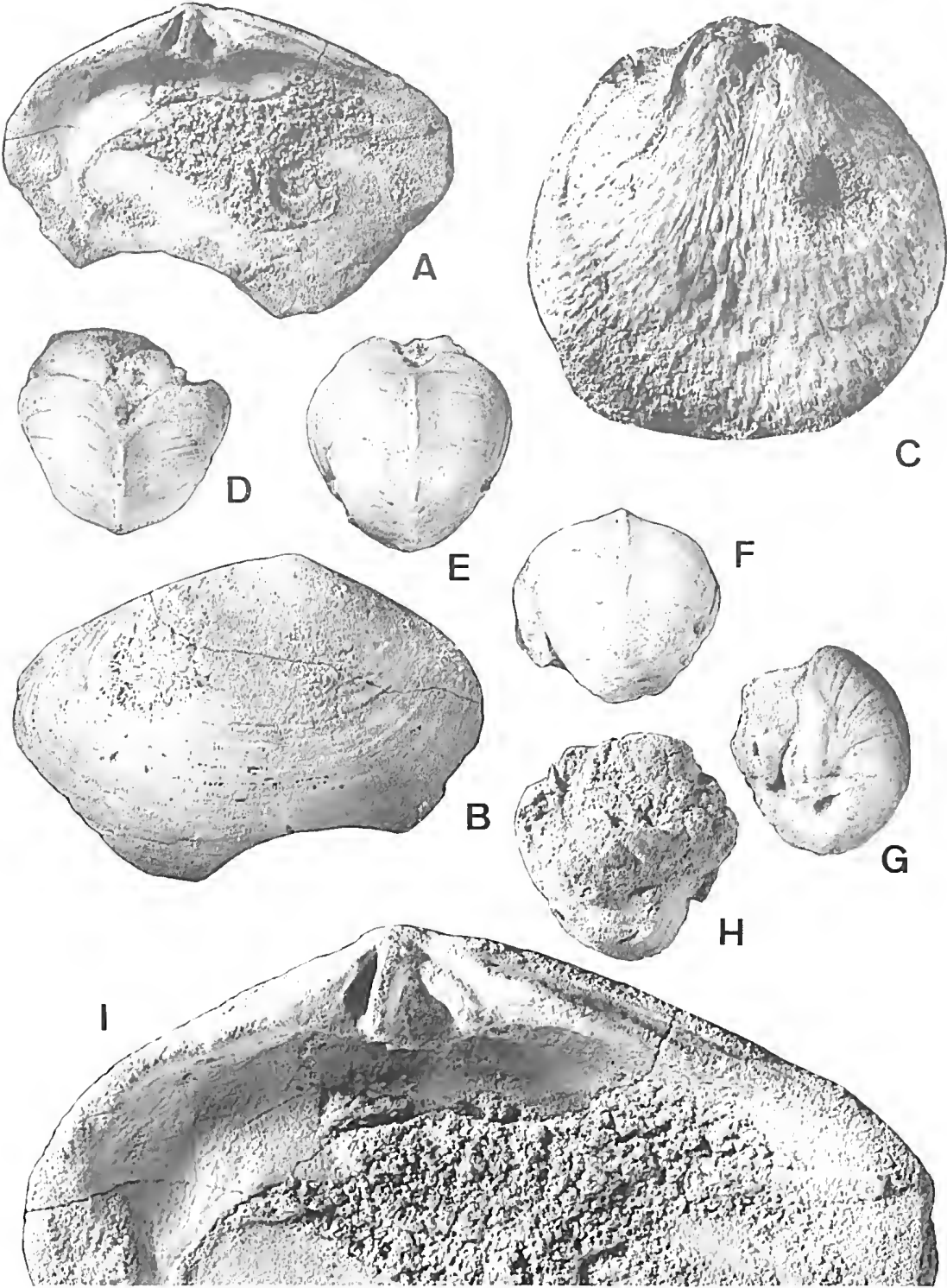
Class GASTROPODA

Superfamily BELLEROPHONTACEA
McCoy, 1851

Family BELLEROPHONTIDAE McCoy, 1851

Genus **Bellerophon** Denys de Montfort, 1808

Type species. *Bellerophon vasulites* Denys de Montfort, 1808, see Knight (1941: 52–54, pl. 11, fig. 3a–e).

Bellerophon pennatus Etheridge, 1907

Fig. 1D–H

Bellerophon—Etheridge, 1895: 33.
Bellerophon sp.—Etheridge, 1897: 16, pl. 1, figs 14, 15.
Bellerophon costatus var. *pennatus*, var. nov.—Etheridge, 1906: 41 (*nomen nudum*).
Bellerophon costatus—J. de C. Sby, var. *pennatus*, var. nov.—Etheridge, 1907: 10, pl. 7, figs 5–7.
Bellerophon pennatus Eth.,Thomas 1957: 180.
Bellerophon pennatus Eth., Thomas 1958: 2.

Lectotype. It is not clear from Etheridge's description of his variety *pennatus* how many specimens he had before him. He does, however, provide a clue that more than one specimen was included within the variety when he stated that 'this form has already been figured from imperfect material' (Etheridge 1907: 10), in reference to his 1897 report. We therefore designate the single specimen he figured in 1907 (pl. 7, figs 5–7) as the lectotype of the variety and raise the variety to species status as a distinctive species of Australian Permian *Bellerophon*. The specimen is registered as NMV P30031 in the collections of the Museum of Victoria.

Comments. The species is differentiated from other Western Australian species described by Dickins (1963) by its moderately narrow sinus, narrow slit and relatively sharp ridge at the slit band. Fine growth lines are distinct and are progressively well marked towards the aperture.

Phylum BRACHIOPODA

Class ARTICULATA

Superfamily AULOSTEGACEA
Muir-Wood & Cooper, 1960

Family AULOSTEGIDAE
Muir-Wood & Cooper, 1960

Genus **Megasteges** Waterhouse, 1975

Type species. *Megasteges nepalensis* Waterhouse, 1975.

Megasteges septentrionalis (Etheridge, 1907)

Fig. 1C

Aulosteges baracoodensis—Etheridge, 1906: 41.
Aulosteges baracoodensis var. *septentrionalis*—Etheridge, 1907: 6, pl. 1, figs 1–5.
Megasteges septentrionalis—(Etheridge)—Archbold, 1986: 49, fig. 1A–F (with synonymy).
Megasteges septentrionalis—(Etheridge Jnr)—Archbold et al., 1993: 226, pl. 32, figs 7, 10, 11.

Lectotype. South Australian Museum specimen P2135, an internal mould of a conjoined shell, figured and selected by Archbold (1986: 49, fig. 1A, B).

Comments. When re-establishing the species, Archbold (1986: 51) noted that one internal mould of a ventral valve, figured by Etheridge (1907, pl. 1, fig. 3) could not be located. It is housed in the collections of the Museum of Victoria with the registered number NMV P30708 and is refigured herein (Fig. 1C). The specimen is typical of the species as redescribed by Archbold (1986).

REFERENCES

ARCHBOLD, N. W., 1981. Studies on Western Australia Permian brachiopods 2, The family Rugosochonetidae Muir-Wood 1962. *Proceedings of the Royal Society of Victoria*, 93: 109–128.

ARCHBOLD, N. W., 1986. *Megasteges septentrionalis* (Etheridge, 1907), a Permian brachiopod from the Northern Territory redescribed. *Proceedings of the Royal Society of Victoria*, 98: 49–51.

ARCHBOLD, N. W., 1988. Studies on Western Australian Permian brachiopods 8, The Late Permian brachiopod fauna of the Kirkby Range Member, Canning Basin. *Proceedings of the Royal Society of Victoria*, 100: 21–32.

ARCHBOLD, N. W., 1993. A zonation of the Permian brachiopod faunas of Western Australia. In *Gondwana Eight, Assembly, Evolution and Dispersal*, R. H. Findlay, A. Unrug, M. R. Banks & J. J. Veevers, eds, A. A. Balkema, Rotterdam, 313–321.

ARCHBOLD, N. W., 1995. Ufimian (early Late Permian) brachiopods from the Perth Basin, Western Australia. *Memoir of the Association of Australasian Palaeontologists*, 18: 153–163.

ARCHBOLD, N. W. & DICKINS, J. M., 1996. Permian (Chart 6). In *An Australian Phanerozoic Timescale*, G. C. Young & J. R. Laurie, eds, Oxford University Press, Melbourne, 127–135.

ARCHBOLD, N. W. & THOMAS, G. A., 1993. *Imperiospira*, a new Western Australia Permian Spiriferidae (Brachiopoda). *Memoir of the Association of Australasian Palaeontologists*, 15: 313–328.

ARCHBOLD, N. W., THOMAS, G. A. & SKWARKO, S. K., 1993. Brachiopods. *Bulletin of the Geological Survey of Western Australia*, 136: 45–51, 196–264 and microfiche supplement.

BOYD, D. W. & NEWELL, N. D., 1968. Hinge grades in the evolution of crassatellacean bivalves as revealed by Permian genera. *American Museum Novitates*, 2328: 1–52.

BOYD, D. W. & NEWELL, N. D., 1977. An addition to the known geographic range of the Permian pelecypod *Oriocrassatella*. *University of Wyoming, Contributions to Geology*, 16: 55–57.

CHAPMAN, F., 1924a. List of fossils from West Kimberley. Western Australia, *Annual Progress Report of the Geological Survey for the year 1923*, 35–36.

CHAPMAN, F., 1924b. Preliminary report on a collection of fossils made by Dr A. Wade in Western Australia and the Northern Territory. In *The Wade Collection of Fossils*, H. J. Green, Government Printer, Melbourne, 3–10.

CHAPMAN, F., 1924c. Table of upper and lower Carboniferous fossils from the Fitzroy River Area. *Commonwealth of Australia, Senate, Parliamentary Paper* 142: 19–20.

CAMPBELL, K. S. W. & McKELVEY, B., 1972. The geology of the Barrington District, NSW. *Pacific Geology*, 5: 7–48.

CLARKE, M. J., 1987. Late Permian (late Lymingtonian =?Kazanian) brachiopods from Tasmania. *Alcheringa* 11: 261–289.

CLARKE, M. J. & FARMER, N., 1976. Biostratigraphic nomenclature for Late Palaeozoic rocks in Tasmania. *Papers and Proceedings of the Royal Society of Tasmania*, 110: 91–109.

CONDON, M. A., 1954. Progress report on the stratigraphy and structure of the Carnarvon Basin, Western Australia. *Report of the Bureau of Mineral Resources, Geology and Geophysics, Australia* 15: 1–163.

CONDON, M. A., 1967. The geology of the Carnarvon Basin, Western Australia, Part 2: Permian Stratigraphy. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Australia*, 77: 1–191.

DENYS DE MONTFORT, P., 1808. *Conchyliologie systématique, et classification methodique des coquilles; offrant leurs figures, leur arrangement générique, leurs descriptions caracteristiques, leurs noms; ainsi que leur synonymie en plusieurs langues,* Tome 1, Coquilles univalves, cloisonnees. Paris, P. Schoell.

DICKINS, J. M., 1956. Permian pelecypods from the Carnarvon Basin, Western Australia. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics*, Australia, 29: 1–55.

DICKINS, J. M., 1961. Permian pelecypods newly recorded from eastern Australia. *Palaeontology*, 4: 119–130.

DICKINS, J. M., 1963. Permian pelecypods and gastropods from Western Australia. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics*, Australia, 63: 1–203.

DICKINS, J. M., 1994. Permian bivalve faunas – stratigraphical and geographical distribution. In *Douzieme Congres International de la Stratigraphie et Geologie du Carbonifere et Permien*, Buenos Aires, Comptes Rendus, vol. 1: 523–536.

DICKINS, J. M., ARCHBOLD, N. W., THOMAS, G. A. & CAMPBELL, H. J., 1989. Mid-Permian Correlation. In *Onzieme Congres International de Stratigraphie et de Geologie du Carbonifere*, Beijing, Compte Rendu, Tome 2: 185–198.

DICKINS, J. M., ROBERTS, J. & VEEVERS, J. J., 1972. Permian and Mesozoic geology of the northwestern part of the Bonaparte Gulf Basin. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Australia*, 116: 17–27.

DICKINS, J. M. & SHAH, S. C., 1979. Correlation of the Permian marine sequences of India and Western Australia. In *Fourth International Gondwana Symposium: Papers (vol. 2)*, B. Laskar & C. S. Raja Rao, eds, Hindustan Publishing Corporation (India), Delhi, 387–408.

DICKINS, J. M. & SKWARKO, S. K., 1981. Upper Paleozoic pelecypods and gastropods from Irian Jaya, Indonesia. *Geological Research and Development Centre, Bandung, Paleontology Series* 2: 43–52.

DICKINS, J. M. & SKWARKO, S. K., 1993. Bivalves. *Bulletin of the Geological Survey of Western Australia*, 136: 52–54, 266–282 and microfiche supplement.

ETHERIDGE, R., Jnr, 1895. Official contributions to the Palaeontology of South Australia, Preliminary report on fossils collected in the North Territory by H. Y. L. Brown, Esq., Government Geologist. *South Australia, House of Assembly, Parliamentary Paper*, 1895, 82: 33–34.

ETHERIDGE, R., Jnr, 1897. Official contributions to the Palaeontology of South Australia, no. 10, The Permo-Carboniferous fossils of Treachery Bay, Victoria River. *South Australia, House of Assembly, Parliamentary Paper 1897*, 127: 14–16, pl. 1.

ETHERIDGE, R., Jnr, 1906. Official contributions to the Palaeontology of South Australia, no. 15, Preliminary report on other fossils forwarded to me by the Government Geologist of South Australia. *South Australia, House of Assembly, Parliamentary Paper 1906*, 55: 41–42.

ETHERIDGE, R., Jnr, 1907. Official contributions to the Palaeontology of South Australia, nos 17–22,

South Australia, House of Assembly, Parliamentary Paper 1907, 54: 1–21, pls 1–12.

GOLOVKINSKIY, N. A., 1868. O Permskoi formatsii v' tsenral'noi chasti Kamsko-Volshskago Basseina. *Materialy po Geologii Rossii*, 1: 275–415, pls 1–5.

GONZALEZ, C. R., 1976. *Oriocrassatella y Stutchburia* (Bivalvia), en la ingresion marina del Permico inferior de la Quebrada de Agua Negra, Depto Iglesia, Prov. de San Juan (Argentina). *Ameghiniana*, 13: 127–140.

GONZALEZ, C. R., 1982. Bivalvos de la formacion Agua del Jaguel, Permico inferior de Mendoza (Argentina). *Ameghiniana*, 19: 367–376.

GUPPY, D. J., LINDNER, A. W., RATTIGAN, J. H. & CASEY, J. N., 1958, The geology of the Fitzroy Basin, Western Australia, *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics*, Australia, 36: 1–116.

HAMLET, B., 1928. Permische Brachiopoden, Lamellibranchiaten und Gastropoden von Timor. *Jaarboek van het Mijnwezen in Nederlandsch-Indie*, 56, 2: 1–115, pls 1–12.

KANEV, G. P., 1994. *Permskie dvustvorchatye Mollyuski gryady Chernysheva*. Rossiiskaya Akademya Nauk, Ural'skoe Otdelenie, Komi Nauchnyi Tsentr, Institut Geologii, Syktyvkar, pp. 1–80, pls 1–6.

KNIGHT, J. B., 1941. Paleozoic gastropod genotypes. *Geological Society of America, Special Paper* 32: 1–510.

LIU, N.-P. & CUI, X.-S., 1983. Discovery of *Eurydesma* –fauna from Rutog, northwest Xizang (Tibet), and its biogeographic significance. *Earth Science, Journal of Wuhan College of Geology*, 1983, 1: 79–92.

LOBANOVA, O. V., 1961. Permskie peletsipody Grodekovskogo raiona zapadnogo Primor'ya. *Sbornik Statei po Paleontologii i Biostratigrafii*, 25: 52–80.

LOGAN, A., 1967. The Permian Bivalvia of northern England. *Palaeontographical Society Monograph*, 121, 518: 1–72, pls 1–10.

MANCENIDO, M. O., GONZALEZ, C. R. & DAMBORENEA, S. E., 1976. La fauna de la Formacion del Salto (Palcozoico superior de la Provincia de San Juan). Parte III: Bivalvia 2. *Ameghiniana* 13: 85–106.

MAXWELL, W. G. H., 1964. The geology of the Yarrol Region. Part 1. Biostratigraphy. *Papers, Department of Geology University of Queensland*, 5, 9: 1–79.

MUROMTSEVA, V. A., 1984. Permskie morskie otlozheniya i dvustvorchatye mollyuski Sovetskoi Arktiki. *Trudy Vsesoyuznyi ordena Trudovogo Krasnogo Znameni Neftyanoi Nauchno-Issledovatel'skii Geologorazvedochnyi Institut*, Nedra, Leningrad. 1–154, pls 1–53.

NEWELL, N. D., 1955. Permian pelecypods of east Greenland. *Meddelelser om Gronland*, 110, 4: 1–34, pls 1–5.

NEWELL, N. D., 1958. A note on Permian crassatellid pelecypods. *American Museum Novitates*, 1878: 1–6.

PLAYFORD, P. E., COPE, R. N., COCKBAIN, A. E., LOW, G. H. & LOWRY, D. C., 1975. Phanerozoic. *Memoir of the Geological Survey of Western Australia*, 2: 223–433.

PRENDERGAST, K. L., 1935. Some Western Australian Upper Palaeozoic fossils. *Journal of the Royal Society of Western Australia*, 21: 9–35.

REED, F. R. C., 1932. New fossils from the Agglomeratic Slate of Kashmir. *Memoirs of the Geological Survey of India, Palaeontologia Indica, New Series*, 20, 1: 1–79, pls 1–13.

ROCHA-CAMPOS, A. C., 1970. Moluscos Permianos da Formacao Rio Bonito (Subgrupo Guata) SC. *Departamento Nacional de Prodocao Mineral, Divisao de Geologica e Mineralogia Boletim*, 251: 1–89.

SKWARKO, S. K., 1993a. The Permian System. *Bulletin of the Geological Survey of Western Australia*, 136: 1–3 + microfiche supplement.

SKWARKO, S. K., 1993b. A list of Permian fossils from the Collie, Perth, Carnarvon and Canning Basins. *Bulletin of the Geological Survey of Western Australia*, 136: 89–109.

SUVEIZDIS, P. I., 1975. Permskaya Sistema Pribaltiki (fauna i stratigrafiya*). Trudy Litovskii Nauchno-Issledovatel'skii Geologorazvedochnyi Institut*, Vypusk 29: 1–305.

TEICHERT, C., 1941. Upper Paleozoic of Western Australia: Correlation and paleogeography. *Bulletin of the American Association of Petroleum Geologists* 25: 371–415.

TEICHERT, C., 1951. The marine Permian faunas of Western Australia (an interim review). *Paläontologische Zeitschrift* 24: 76–90.

TEICHERT, C., 1952. Carboniferous, Permian and Jurassic in the northwest Basin, Western Australia. In *Symposium sur les series de Gondwana, XIXe Congrès Geologique International, Alger 1952*, 115–135

TEICHERT, C., 1957. Notes on the geology of the Carnarvon (Northwest) Basin, Western Australia. *Journal of the Royal Society of Western Australia*, 40: 65–72.

TERMIER, G., TERMIER, H., DE LAPPARENT, A. F. & MARIN, P., 1974. Monographie du Permo-Carbonifere de Wardak (Afghanistan Central). Documents des Laboratoires de Geologie de la Faculte des Sciences de Lyon, Hors Serie, 2: 1–167, pls 1–38.

THOMAS, G. A., 1957. Oldhaminid brachiopods in the Permian of Northern Australia. *Journal of the Palaeontological Society of India*, 2: 174–182.

THOMAS, G. A., 1958. Stratigraphy and palaeontology of the Port Keats Area, Northern Territory. *Australian and New Zealand Association for the Advancement of Science, 1958 Congress, Section C, Abstracts, Lectures, Papers*, pp. 1–5.

THOMAS, G. A. & DICKINS, J. M., 1954. Correlation and age of the marine Permian formations of Western Australia. *Australian Journal of Science*, 16: 219–223.

WANNER, C., 1940. Neue Permische Lamellibranchiaten von Timor. In *Geological Expedition of the University of Amsterdam to the Lesser Sunda Islands in the southeastern part of the Netherlands East Indies 1937 under leadership of H. A. Brouwer*, vol. 2: 369–395, pl. 1.

WATERHOUSE, J. B., 1975. New Permian and Triassic brachiopod taxa. *Papers, Department of Geology University of Queensland*, 7, 1: 1–23.

YAKOVLEV, N. N., 1902. Paleozoiskii predstavitel' Crassatellidae. *(Schizodus planus* Golowk.*).* *Izvestiya Geologicheskogo Komiteta*, 21, 9: 755–760, pl. 10.

YAKOVLEV, N. N., 1928. *Procrassatella,* novyi rod iz Permi. *Ezhegodnik Russkogo Paleontologicheskogo Obshchestva*, 7: 119–125.

EARLY DEVONIAN (EMSIAN) AGGLUTINATED FORAMINIFERANS FROM BUCHAN AND BINDI, VICTORIA, AUSTRALIA

K. N. BELL

Museum of Victoria, Swanston Street, Melbourne, Victoria 3000

BELL, K. N., 1996:12:31. Early Devonian agglutinated foraminiferans from Buchan and Bindi, Victoria, Australia. *Proceedings of the Royal Society of Victoria* 108 (2): 73–106. ISSN 0035-9211.

Twenty-six genera and 45 species of Early Devonian (Emsian) agglutinated foraminiferans are described from the Taravale Formation and Buchan Caves Limestone from eastern Victoria. Three new genera, *Cystringarhiza*, *Patellammina* and *Cylindrammina* are described and 28 new species: *Cystringarhiza mawsonae*, *C. corona*, *C. tribracchia*, *C. furca*, *Astrorhiza triquetra*, *As. constans*, *As. sinus*, *Cylindrammina stolonifera*, *Hyperammina reflua*, *H. proboscis*, *Rhabdammina proavita*, *Saccorhiza surculus*, *Stomasphaera cyclops*, *Patellammina prona*, *Hormosina divitiae*, *Reophax troca*, *Lagenammina talenti*, *L. laxacolla*, *L. ovata*, *Lituotuba torquata*, *L. helix*, *Thurammina zaramama*, *Webbinelloidea crassus*, *Pelosina grandaeva*, *Kerionammina prolata*, *Tolypammina anguinea*, *T. tantula*, *Ammovertella calyx*.

THE FORAMINIFERANS described in this paper came from the Early Devonian Buchan Caves Limestone and the Taravale Formation of the Buchan and Bindi areas of East Gippsland, Victoria (Figs 1, 2).

No detailed work has been carried out on the Victorian Devonian foraminiferans although they have previously been mentioned by Chapman (1933) and Teichert & Talent (1958): Chapman (1933) described two species, one from Mitcham as *Trochammina busaria*, later referred by Conkin & Conkin (1968) to *Thuramminoides sphaeroidalis* Plummer, and one as *Hemigordius lilydalensis* (however this species is arenaceous and does not belong in the calcareous genus *Hemigordius*). Teichert & Talent (1958) quoted W. J. Parr in reporting the presence of very poorly preserved unidentified foraminiferans in acid residues of the Taravale Formation. Conkin & Conkin (1968) listed, without discussion, the presence of *Tolypammina* spp., *Sorosphaeroidea* sp. and *Hyperammina*(?) sp. from the Devonian Pyramid Member of the Buchan Caves Limestone at Bindi.

MATERIAL

Over the past few years Ruth Mawson (Macquarie University, N.S.W.) has studied the conodont faunas of the Taravale Formation from Buchan and Bindi areas of East Gippsland (Mawson 1987a). It was from the light flotation fraction of the acetic acid-digested limestones and marls of this material that the present study of the foraminiferan faunas was undertaken.

Approximately 350 samples were available with the sample size varying from about 30 g up to 250 g. Of these, fewer than 90 samples had any foraminiferans present at all and in only 14 samples were foraminiferans frequent. Specimens were picked from the residues as conventional flotation methods were not successful.

REGIONAL GEOLOGY AND STRATIGRAPHY

The extensive Lower Devonian sediments about Buchan and Bindi have been described in detail by Fletcher (1963), Gaskin (1933), Mawson (1987a), Mawson et al. (1985), Philip (1966), Talent (1956, 1965, 1967, 1969) and Teichert & Talent (1958). For detailed maps, locality data and stratigraphy for the samples studied here see Mawson (1987a) and Figs 1–3 herein.

Lithologically, the Taravale Formation consists of 'impure limestone nodules and irregular, discontinuous limestone beds in mudstones' (Mawson 1987a). The Buchan Caves Limestone, which underlies the Taravale Formation, consists essentially of basal dolomitic limestones overlain by dark, fine-grained calcarenites (Talent 1956, 1969). The Murrindal Limestone is a small lenticular limestone body deposited during a gradual regressive event (Talent 1989) and lies entirely within the *perbonus* Zone. The Buchan Caves Limestone is thought to have been deposited on a shallow, flat, wide shelf (the Buchan-Indi-Combienbar Shelf) (Talent 1965, 1969, 1989). Slow increases in depth occurred; in the Buchan area as demonstrated by the faunal changes (Talent 1956), and at Bindi where five conodont biofacies have been distinguished (Mawson et al. 1993).
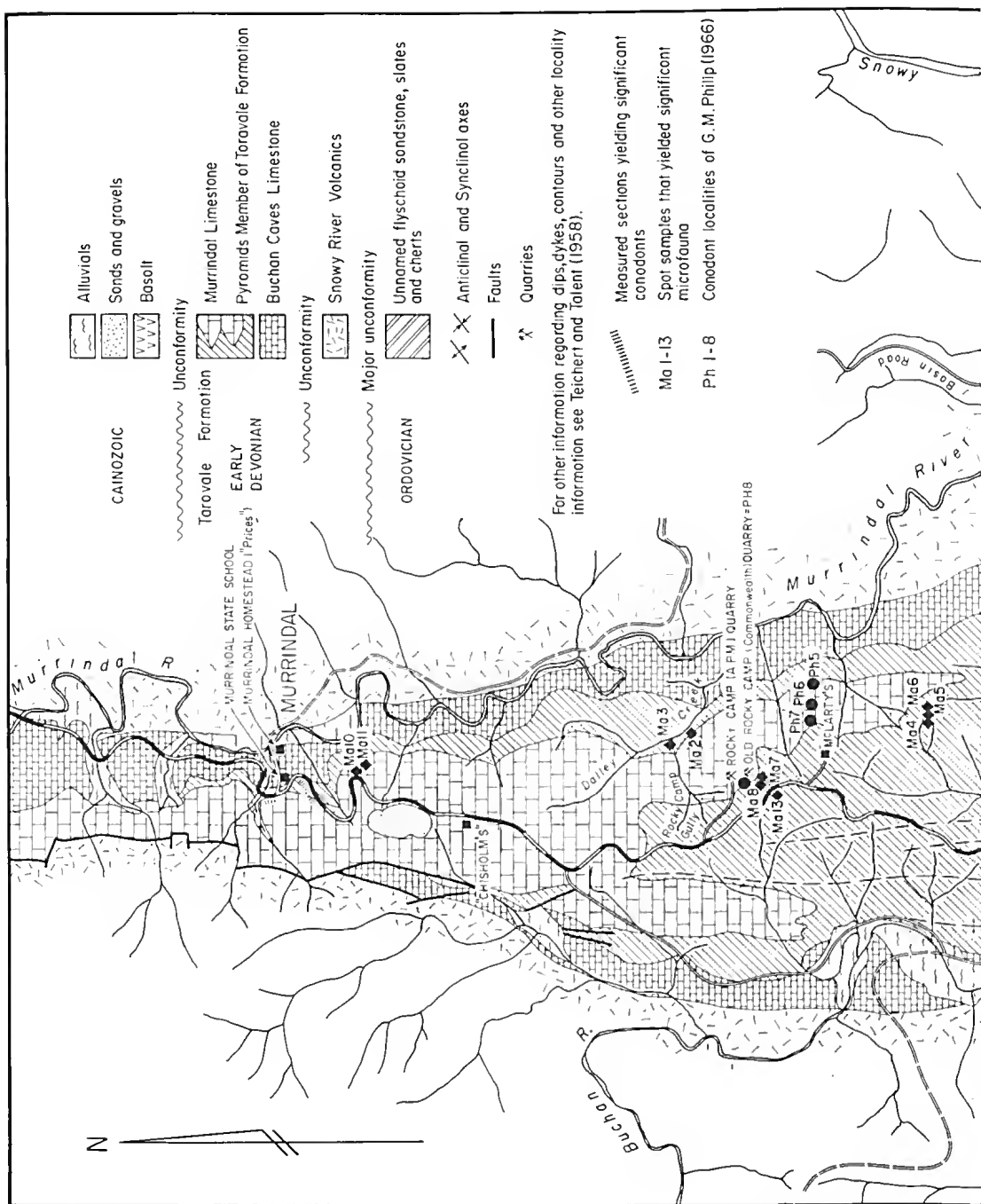
Fig. 1. The Buchan Group in the Buchan–Murrindal Area, Eastern Victoria, showing location of sample sites
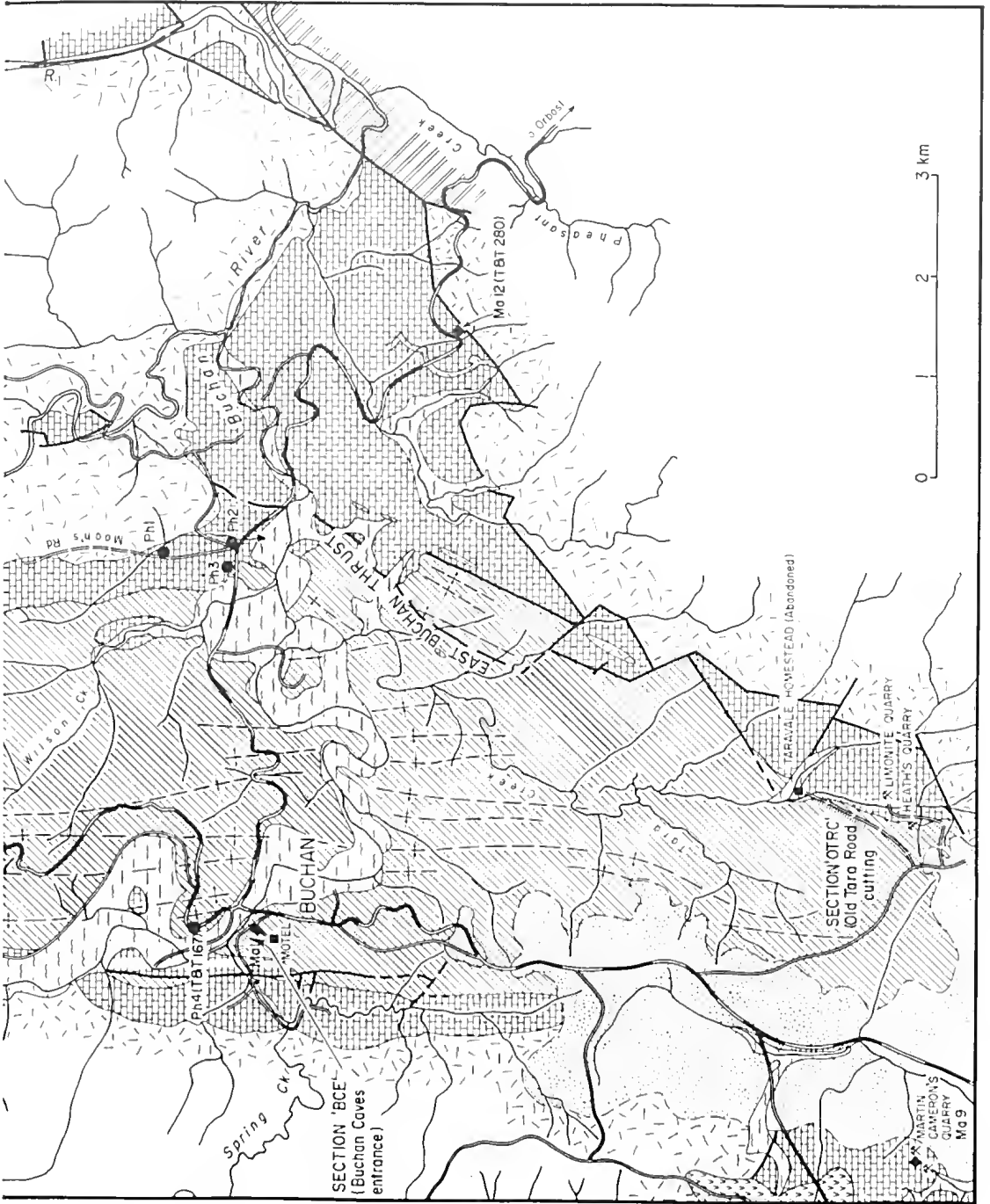
OTRC, ORCQ and Ma 13 (after Mawson 1987).

QUATERNARY — Alluvials

~~~~~~~~ unconformity

LATE DEVONIAN — Mt Tambo Beds — non-marine sandstones, conglomerates and siltstones

~~~~ unconformity

TARAVALE FORMATION — Shanahan Limestone (name to be formalized)

Buchan Caves Limestone (basal dolomitic facies not discriminated)

EARLY DEVONIAN ~~~~ unconformity

Snowy River Volcanics — acid, often ignimbritic extrusives

~~~~~~~~ unconformity

SILURIAN — Mount Waterson Formation — conglomerates and sandstones

Old Hut Limestone

~~~~~~~~ unconformity

Omeo Metamorphic Complex — principally metamorphosed Ordovician and perhaps some Silurian flyschoid sandstones and siltstones

—— faults

.... measured sections yielding significant conodonts in this survey

• 1-36 brachiopod-coral localities, mainly of the Taravale Formation (only to yielded significant conodont faunas)

main roads
minor roads
jeep track

Geological and topographical base from mapping by J.A.Talent (1966 unpub, 1967)

Blackfellows Flat

Tambo River

Mt Shanahan

Section 'SB' (South Blackfellows)

Mt Waterson

Old Hut Creek

CARRABUNGLA FAULT

BINDI FAULT

34

35
36

Old Paddock Creek

Armett's Bindi Homestead

to Nunyong Plains

Bindi Creek

Section 'BON' (Bonanza Gully)

Bourke's

Harding's

21

6
5
4

3
2
10

22

3
12 11

23
24

8
9

3 7

to Omeo and Smith's Creek

19

Limestone Creek (Dry Gully)

Section 'SALC' (South Arm of Limestone Creek)

14

20

15

16
18
17

33

25
26
27
28

32

30

Lee's

29

Junction Creek

31

BINDI FAULT

0   1   2   3 km

The Taravale Formation represents a diachronous transgressive phase which took place during the *dehiscens* Zone at Buchan but which occurred within the *perbonus* Zone at Bindi (Mawson 1987a). There occurred a greater input of insoluble clastic material leading to the deposition of impure limestones and mudstones. VandenBerg (1988) has suggested that this was due to uplift of the Buchan–Indi–Combienbar Shelf. He also suggested that the Rocky Camp Limestone was a very shallow-water carbonate bank.

These sediments contain a diverse marine fauna of brachiopods (Talent 1956), molluscs (Talent 1956; Teichert & Talent 1958), ostracoda (Krommelbein 1954), corals (Hill 1950; Pedder 1967a, 1967b), ammonites (Teichert 1948), stromatoporoids (Ripper 1937; Webby et al. 1993) and conodonts (Mawson 1987a; Philip 1966).

The early studies pointed to an Emsian age; with the more detailed conodont studies (Mawson et al. 1985; Mawson 1987a) it is now known that these sediments belong to the *dehiscens*, *perbonus–gronbergi*, *inversus* and *serotinus* zones of the Early Devonian, i.e. upper Pragian to upper Emsian Stages.

The foraminiferans described herein, with about 70% being regarded as new species, represent an assemblage that is endemic, as far as is presently known, to the Buchan–Bindi area. Therefore they cannot of themselves serve as an aid for stratigraphical correlation.

Fig. 3. Stratigraphic ranges of the Emsian (Early Devonian) sequences investigated in this report. For detailed stratigraphic information see Mawson (1987a).

AGES OF SECTIONS STUDIED

Old Taravale Road cutting (OTRC): *Polygnathus dehiscens dehiscens* occurs throughout this section but whilst forms transitional to *P. perbonus* are present, *P. perbonus* itself does not occur (Mawson 1987a). Thus this section lies wholly within the *dehiscens* Zone.

Bonanza Gully, Bindi (BON): In this section *P. dehiscens dehiscens* is found in a short interval from sample 25–27.5 (123.9–125 m above base) to sample 46–50 (129.6–131.5 m above base) with *P. perbonus* first occurring in sample 46–50 and persisting in higher samples (Mawson et al. 1993). In samples below the first occurrence of *P. dehiscens dehiscens*, *Ozarkodina prolata* is common and, as this species is not known to occur in sediments below the *P. dehiscens* Zone (Mawson 1987b), the BON sequence ranges from the *dehiscens* to *perbonus* zones.

Ma 13, Gelantipy Road: This sample is the same as 28 on the Gelantipy Road section (Mawson 1987a). Elements of forms transitional to *P. inversus* and of *P. inversus* occur thus placing it within the *inversus* Zone; *P. pseudoserotinus* which is broadly coeval with *serotinus* (Mawson 1987a) first occurs some 250 m stratigraphically higher.

Old Rocky Camp Quarry (ORCQ): This sample came from 10–15 m above the top of the Murrindal Limestone and is considered to be at the very top of the *perbonus* Zone (J. A. Talent, pers comm.).

South arm, Limestone Creek (SALC): The lower part of this section (samples 8, 9) yielded no conodonts but the upper part (samples 7-2) contained elements transitional to *P. setotinus* with samples 6-4 containing *P. serotinus* (Mawson 1987a); thus this section is considered to straddle the *inversus–serotinus* boundary.

SYSTEMATIC PALAEONTOLOGY

All types and figured specimens have been deposited in the Palaeontological collections of the Museum of Victoria, registered numbers prefixed NMV P.

Note on the term *proloculum*: In recent years there has been a tendency to call the initial chamber of a foraminiferan test the proloculus (e.g. Loeblich & Tappan 1994). However Cushman

Fig. 2. The Buchan Group in the Bindi Area, Eastern Victoria, showing location of sample sites BON and SALC (after Mawson 1987).

	OTRC			BON								ORCQ	Ma13	SALC		
	2	5	7	13-15	29-35	36-39	39-44	56-60.5	60.5-65	206	220-240	10-15		9	7	4
Astra. triquetra			x											x		
Astra. constans				x								x	x	x	x	
Astra. sinus												x		x	x	
Cyst. mawsonae													x	x		
Cyst. tribracchia												x		x	x	
Cyst. corona												x	x	x	x	
Cyst. furca		x										x	x	x	x	x
C. stolonifera						x						x		x	x	
R. linearis				x									x	x	x	
R. proavita			x													
S. surculus												x				
H. reflua		x				x						x				
H. proboscis												x	x			
H. sp.												x				
P. cava	x		x													
S. sp.cf. S.confusa	x	x	x													
S. cylindrica	x															
S. biosculata												x				
S. cumberlandiae				x		x										
L. sphaerica				x									x	x	x	

	OTRC			BON								ORCQ	Ma13	SALC		
	2	5	7	13-15	29-35	36-39	39-44	56-60.5	60.5-65	206	220-240	10-15		9	7	4
L. stilla													x			
L. talenti												x	x		x	
L. laxacolla						x							x	x	x	
L. ovata												x		x		
S. cyclops											x					
O. eisenacki				x								x				
P. grandaeva												x	x			
T. echinata		x	x			x						x				
T. subsphaerica		x	x	x								x				
T. tributa							x	x								
T. foerstei												x				
T. zaramara									x			x				
Hemisph. sp.			x													
W. crassus										x	x					
M. tholus				x												
P. prona											x					
K. prolata			x									x				
T. anquinea		x	x	x	x	x						x	x			
T. tantula				x	x	x						x				
A. calyx				x								x				

Table 1 continued next page.

	OTRC				BON							ORCQ	Ma13	SALC		
	2	5	7	13-15	29-35	36-39	39-44	56-60.5	60.5-65	206	220-240	10-15		9	7	4
T. torquata			x	x												
L. helix		x														
H. divitiae											x					
R. troca		x	x									x	x			
Th. sphaeroidalis	x	x	x												x	x

Table 1. Distribution of species within samples.

(1905: 538) defined the initial chamber as the proloculum. This definition has been followed in this paper.

The suprageneric classification follows Loeblich & Tappan (1988).

Order FORAMINIFERIDA Eichwald, 1830

Suborder Textulariina Delage & Hérouard, 1896

Family ASTRORHIZIDAE Brady, 1881

Genus **Astrorhiza** Sandahl, 1858

Astrorhiza triquetra n.sp.

Fig. 5A, B

Description. Test free; central body chamber is triangular and slightly inflated, the sides are of equal length; an arm issues from each corner of the central chamber, these stolons lie in one plane and are short, less than half side length; aperture is a simple opening at the end of each stolon; test wall formed of small quartz grains, with little cement, smoothly finished.

Holotype. NMV P126952, from Gelantipy Road, Buchan, sample Ma 13, Taravale Formation.

Measurements
Holotype NMV P126952 body diameter 0.3 mm
Paratype NMV P199385 — Ma 13, 0.46 mm
Paratype NMV P199386 — SALC 9, 0.25 mm
Paratype NMV P199387 — OTRC 7, 0.39 mm

Distribution. Ma 13, OTRC 7, SALC 9; *dehiscens-inversus* Zones.

Remarks. The stolons are usually short, most likely due to breakages after death, as occasionally they are longer (equal to side length) and slightly curved, which may indicate that they were flexible in life.

A. triquetra differs from the Recent *A. triangularis* Earland 1933 from South Georgia in having stout arms, a smaller body chamber with less inflated sides and a much smoother surface.

Derivation of name. triquetra (Latin): three cornered; referring to the triangular shaped body chamber.

Astrorhiza constans n.sp.

Fig. 5C, D

Description. Test free; large, slightly inflated body chamber, with six coplanar stolons issuing more or less regularly about the periphery; the stolons are short and thick, slightly flaring at the

Fig. 4. *Ammovertella calyx* Bell n.sp. Schematic outlines showing the variation in growth pattern. P, proloculum (various magnifications).

apertural end; the aperture is a simple opening at the end of each stolon; the test is formed of small quartz grains, with little cement, and fairly smoothly finished.

Holotype. NMV P126953, from south arm, Limestone Creek, Bindi, sample 7, Taravale Formation.

Measurements
Holotype NMV P126953, body diameter, 0.4 mm
Paratype NMV P199388–BON 13.5-15, 0.34 mm
Paratype NMV P199389–SALC 7, 0.3 mm
Paratype NMV P199390–ORCQ 10-15, 0.6 mm

Distribution. SALC 7, SALC 9, BON 13.5, ORCQ 10-15; *perbonus–inversus* zones.

Remarks. This species differs from *A. triquetra* n.sp. in the number of arms and the shape of the body chamber, and from *A. sinus* n.sp. by the shape of the stolons.

Specimens referred to this species from BON 13.5 and SALC 9 often have one or more stolons stouter than the others and the placement of the arms is then not as regular about the periphery.

Derivation of name. constans (L.): consistent; referring to the regular placement of the stolons.

Astrorhiza sinus n.sp.

Fig. 5E–G

Description. Test free; body chamber discoidal, with five stolons issuing from one side of the chamber; the stolons are long, narrow and may be curved; a simple aperture at the end of each stolon; test wall formed of fine quartz grains with little cement, fairly smoothly finished surface.

Holotype. NMVP 126954, from south arm, Limestone Creek, Bindi, sample 7, Taravale Formation.

Measurements
Holotype NMV P126954, body diameter, 0.38 mm
Paratype NMV P199391–ORCQ 10-15, 0.48 mm

Distribution. SALC 7, ORCQ 10-15, BON 13.5-15; *perbonus–inversus* zones.

Remarks. In the holotype there is only one long, sinuous stolon, the others are short due to breakages, but in specimen NMV P126955 from ORCQ 10-15 two stolons are long and curved, one being somewhat flattened. It is thus possible that all the stolons were originally long and sinuous.

A. sinus n.sp. differs from *A. constans* n.sp. in the body chamber and arm shape and placement and from *A. triquetra* n.sp. in the body shape.

Derivation of name. sinus (L.): winding; referring to the shape of the stolons.

Genus **Cystingarhiza** n. gen.

Genotype. Cystingarhiza mawsonae n.sp. NMV P126956, from south arm, Limestone Creek, Bindi, sample 9, Taravale Formation.

Description. Test free, small, globular to ovate; consisting of a single spherical or subspherical chamber with few (2–6) radiating tubular extensions, not all in the same plane; wall agglutinated of small to medium sized sand grains with little cement visible; apertures at open ends of the tubular extensions.

Distribution. Early Devonian (Emsian; *perbonus-serotinus* zones) of Eastern Australia.

Remarks. This new genus has been erected to accommodate *Astrammina*-like specimens known only from the Early Devonian of Victoria. The genus *Astrammina* Rhumbler (in Wiesner 1931) was erected to accommodate *Astrorhiza*-like specimens but which had a globular, not flattened, central chamber and fewer arms. *Astrammina* is only known from the Holocene in the Antarctic, South Atlantic and South Pacific (Loeblich and Tappan 1988). *Cystingarhiza* differs from *Astrammina* in the much smaller size (about one-quarter to one-tenth diameter) and in having the stolons usually not in the one plane.

Conkin et al. (1968) have suggested that *Thurammina*? *triradiata* Gutschick & Treckman emend. Conkin, Conkin & Canis, of the Mississippian of the U.S.A., may be better referred to *Astrammina* (i.e. the new *Cystingarhiza*), because it has long tubular processes whereas *Thurammina* has smaller stubby papillae.

Derivation of name. *kystrix* (Greek, f.): a cell + *rhiza* (Gk): a root.

Cystingarhiza mawsonae n.sp.

Fig. 5I, J

Description. Test free; moderate size; central chamber globular with five radiating stolons which taper slightly aperturally; simple aperture at the ends of each stolon; test composed of small quartz grains with little cement; coarsely finished.

Holotype. NMV P126956, from south arm, Limestone Creek, Bindi, sample 9, Taravale Formation.

Measurements
Holotype NMV P126956, body chamber diameter
0.24 mm
Paratype NMV P199392—SALC 9, 0.3 mm
Paratype NMV P199393—Ma 13, 0.35 mm

Distribution. SALC 9, Ma 13; *inversus* Zone.

Remarks. The stolons are of variable length due to breakage and range up to equal in length to the central chamber diameter.

Derivation of name. For Dr Ruth Mawson, Macquarie University, for her contributions to the knowledge of Devonian biostratigraphy in Australia.

Cystingarhiza corona n.sp.

Fig. 5K, L

Description. Test free; moderate size; globular central chamber with four radiating stout stolons which issue from one cap of the central chamber; stolons short, about one-third of central chamber diameter; wall composed of fine grains with little cement, surface coarsely finished; aperture not observed on holotype but is a simple opening at the end of each stolon in other specimens.

Holotype. NMV P126957, from south arm, Limestone Creek, Bindi, sample 9, Taravale Formation.

Measurements (in mm)	diam.	arms	aperture
Holotype NMV P126957	0.3	0.09	0.05
Paratype NMV P199394—ORCQ	0.6	0.3	0.12
Paratype NMV P199395—Ma 13	0.43	0.12	0.05
Paratype NMV P199396—SALC 7	0.6	0.18	0.1

Distribution. SALC 7, SALC 9, Ma 13, ORCQ 10–15; *perbonus-inversus* zones.

Remarks. The degree to which the stolons are coplanar varies greatly; in the holotype the arms are almost in one plane whereas in specimens from ORCQ 10–15 the arms are highly angled with respect to the main chamber.

Specimens having only two or three arms are recorded as separate species.

Derivation of name. *corona* (L.): crown; referring to the stolons encircling one cap of the chamber.

Fig. 5. A–B, *Astrorhiza triquetra* Bell n.sp. A, Holotype NMV P126952, ×72, Ma 13. B, Paratype, NMV P199387, ×72, OTRC 7. C–D, *Astrorhiza constans* Bell n.sp. C, Holotype, NMV P126953, ×54, SALC 7. D, Paratype, NMV P199388, ×60, BON 13.5-15. E–G, *Astrorhiza sinus* Bell n.sp. E, Holotype, NMV P126954, ×45, SALC 7 F, Paratype, NMV P199391, ×63, ORCQ 10-15. G, Paratype, NMV P126955, ×36, BON 13.5-15. H, *Cystingarhiza tribrachia* Bell n.sp., holotype, NMV P126958, ×72, ORCQ 10-15. I–J, *Cystingarhiza mawsonae* Bell n.sp. I, Holotype, NMV P126956, ×90, SALC 9. J, Paratype, NMV P199392, ×72, SALC 9. K–L, *Cystingarhiza corona* Bell n.sp. K, Paratype, NMV P1999394, ×36, ORCQ 10-15. L, Holotype, NMV P126957, ×90, SALC 9. M–O, *Cystingarhiza furca* Bell n.sp. M, Paratype, NMV P199398, ×90, SALC 7. N, Holotype, NMV P126959, ×63, SALC 7. O, Paratype, NMV P199399, ×72, SALC 7.

Cystingarhiza tribracchia n.sp.

Fig. 5H

Description. Test free; a small globular chamber from which issues three coplanar stolons; stolons are long, upto twice the body chamber diameter in length, narrow; aperture not observed.

Holotype. NMV P126958, from Old Rocky Camp Quarry, Buchan, sample 10–15 m above the top of Murrindal Formation; Taravale Formation.

Measurements (in mm)	diam.	arm	aperture
Holotype NMV P126958	0.1	0.3	0.05
Paratype NMV P199397–SALC 9	0.09	0.2	0.08

Distribution. ORCQ 10–15, SALC 9; *perbonus-inversus* zones.

Remarks. Tests are known from internal casts only. This species, which could be placed in the genus *Astrorhiza* because of its coplanar stolons, however appears to form a connecting link between *C. mawsonae* (5 stolons) and *C. furca* (2 stolons). Whether the number of stolons is a sufficient character to differentiate these species must await more and better preserved material. Specimens from SALC 9 show curving stolons.

Derivation of name. *tres* (L.): three; *bracchium* (L.): arm-like.

Cystingarhiza furca n.sp.

Fig. 5M–O

Description. Test free; body chamber ellipsoidal, slightly compressed at one end from which issues two stolons; stolons straight and narrow; aperture a simple opening at the end of each stolon; wall is fine grained with little cement, surface smoothly finished.

Holotype. NMV P126959, from south arm, Limestone Creek, Bindi, sample 7, Taravale Formation.

Measurements (in mm)	length × width	arm	aperture
Holotype NMV P126959	0.39 × 0.26	0.19	0.09
Paratype NMV P199398 –SALC 7	0.60 × 0.26	0.15	0.06
Paratype NMV P199399 –SALC 7	0.45 × 0.36	0.15	0.09
Paratype NMV P199400 –SALC 7	0.32 × 0.31	0.13	0.05
Paratype NMV P199401 –ORCQ	0.38 × 0.16	0.07	0.05

Distribution. SALC 7, SALC 9, SALC 4, ORCQ 10–15; *perbonus-serotinus* zones.

Remarks. This species shows much variation both in the shape and inflation of the central chamber and in the divergence angle between the two stolons. The body chamber ranges from quite elongate to almost spherical with subquadrate forms present also. These do not seem to be preservational differences but morphological variations within the species. The angle of divergence between the two stolons varies from 40° to 113°.

Genus **Cylindrammina** n. gen.

Genotype. *Cylindrammina stolonifera* n.sp. NMV P126994, from south arm, Limestone Creek, Bindi, sample 7, Taravale Formation.

Description. Test free; consisting of an inflated tubular chamber usually slightly curved, from which protrude several (2–10) thin, short stolons; wall composed of fine grains, thin, with a slightly rough exterior but smooth interior; a simple aperture occurs at the end of each stolon.

Remarks. *Cylindrammina* n. gen. differs from both *Astrorhiza* and *Cystingarhiza* n.gen. in the tubular shape of the test which can be quite variable in degree of curvature and amount of inflation. It also differs from *Astrorhizoides* Shchedrina, 1969 which consists of a thick, branching tube unlike *Cylindrammina* n. gen. which is a slender, usually curved tube with short thin stolons. The number of stolons per test also is variable within a population from any one sample, varying from two to ten; the stolons appear to be placed at random over the test.

Cylindrammina stolonifera n.sp.

Fig. 6A–C

Description. As for genus.

Holotype. NMV P126994, from south arm, Limestone Creek, Bindi, sample 7, Taravale Formation.

Measurements (in mm)	length	width	stolons no.	diam.
Holotype NMV P126994	0.72	0.3	8	0.06
Paratype NMV P199402 –SALC 7	0.72	0.3	2	0.06
Paratype NMV P199403 –ORCQ	0.8	0.6	4	0.16
Paratype NMV P199404 –SALC 9	0.78	0.21	3	0.1

Distribution. SALC 7, SALC 9, ORCQ 10–15, BON 36–39; *dehiscens-inversus* zones.

Remarks. The length of the stolons is variable and the shortness of the majority of them is most likely due to breakages as odd specimens from BON 36–39 and SALC 9 show longer arms than normally found.

Derivation of name. *stolonifera*: referring to the side arms.

Genus **Rhabdammina** M. Sars in Carpenter 1869

Rhabdammina linearis Brady, 1879

Fig. 6G–l

Rhabdammina linearis Brady, 1879: 37, pl. 3, figs 10–11.—Brady 1884: 26, pl. 22, figs 1–6.

Description. Test free; large ellipsoidal chamber with two diametrically opposed long, straight, tubular stolons issuing from the narrower ends of the main chamber; aperture a simple opening at the ends of each stolon; wall finely arenaceous, roughly finished.

Measurements (in mm)		diam. chamber	tube diam.
Figured specimen	NMV P126960	0.32	0.1
Figured specimen	NMV P199405		
	—Ma 13	0.3	0.1
Unfigured specimen	NMV P199406		
	—BON 13.5–15	0.16	0.09
Figured specimen	NMV P199407		
	—BON 13.5–15	0.22	0.07
Unfigured specimen	NMV P199408		
	—SALC 7	0.26	0.08
Unfigured specimen	NMV P199409		
	—SALC 7	0.6	0.17

Distribution. SALC 7, Ma 13, BON 13.5–15; *perbonus-inversus* zones.

Remarks. There seems to be nothing to distinguish these early Devonian specimens from Brady's Recent species that cannot be assigned to preservational differences e.g. shorter stolons due to breakages and the slight compression of some specimens. Some specimens do have a more inflated central chamber than the Recent forms.

Rhabdammina proavita n.sp.

Fig. 6F

Description. Test free; small globular prolocular chamber from which two arms issue diametrically; the arms are only slightly narrower than the central chamber, and branch a short distance from the chamber; these secondary stolons are usually narrower than the primary ones; aperture is a simple opening at the ends of the stolons; wall formed of very fine quartz grains, with little cement; surface very smoothly finished.

Holotype. NMV P126961, from Old Taravale Road Cutting, Buchan, sample 7, Taravale Formation.

Measurements (in mm)	prolocular diam.	primary arm diam.
Holotype NMV P126961	0.2	0.18
Paratype NMV P199410—OTRC 7	0.1	0.07

Distribution. Known only from the type locality, OTRC 7; *dehiscens* Zone.

Remarks. In general shape this species is similar to the Recent species, *Rhabdammina cornuta* Brady, but differs in the smooth surface texture and the very fine grains used in the test wall.

R. proavita shows some variation in the size of the central chamber, the length of the primary stolons and the nature of the secondary arms. In some specimens the primary arms may not branch but instead become flaring and flattened, although this may be a preservational artefact in part.

Derivation of name. *proavita* (L.): ancestral.

Genus **Saccorhiza** Eimer and Fickert, 1899

Saccorhiza surculus n.sp.

Fig. 6D, E

Description. Test free; a relatively large, flattened proloculum followed by a narrow cylindrical tube of nearly uniform diameter, which bifurcates once; test wall is finely arenaceous with a fairly smooth surface; aperture is a rounded opening at the end of each branch.

Holotype. NMV P126962, from Old Rocky Camp Quarry, Buchan, sample 10–15 m above the Murrindal Limestone, Taravale Formation.

Measurements (in mm)	length	arm width	
		primary	secondary
Holotype NMV P126962	0.21	0.02	0.01
Paratype NMV P199411			
—ORCQ	0.25	0.02	0.02

Distribution. Known only from the type locality, ORCQ 10–15; *perbonus* Zone.

Remarks. Hofker (1972) has considered *Saccorhiza* to be a subgenus of *Hyperammina* on the basis of the globular proloculum and the presence of rare abnormal ramifying forms of several otherwise typical *Hyperammina*. Here it is considered that although the two genera are closely related the bifurcation of the test is sufficient to distinguish *Saccorhiza* from *Hyperammina*. The presence or absence of sponge spicules in the test wall is only a specific character.

None of the recovered specimens showed a typical globular proloculum; in all cases this part of the test was flattened and distorted to varying degrees.

Derivation of name. *surculus* (L.): a young shoot or twig; referring to the fancied resemblance of the species.

Genus **Hyperammina** Brady, 1878

Hyperammina reflua n.sp.

Fig. 7C, D

Description. Test free; globular to subglobular proloculum followed by a long tubular second chamber which is narrower than the proloculum and separated from it by a slight constriction; this tubular chamber is turned back on the proloculum initially for about one-third of a whorl and then becomes more or less linear; near the apertural end, the tubular chamber becomes reflexed for about one-quarter of its length; the second chamber is of more or less uniform diameter until near the aperture when it narrows and then widens to a simple circular aperture; wall formed of fine sand grains, with a smoothly finished surface.

Holotype. NMV P126963, from Old Rocky Camp Quarry, Buchan, sample 10–15 paces above the Murrindal Limestone, Taravale Formation.

Measurements (in mm)	proloculum diam.	tube diam.	length
Holotype NMV P126963	0.12	0.07	1.08
Paratype NMV P199412 −ORCQ	0.08	0.18	1.02
Paratype NMV P199413 −BON 36–39	0.14	0.14	1.26

Distribution. ORCQ 10–15, OTRC 5, OTRC 7, BON 36–39; *dehiscens–perbonus* zones.

Remarks. The placement of this and the next species (*H. proboscis* n.sp.) in the genus *Hyperammina* is based on the globular proloculum and the tubular chamber which suggests placement in *Hyperammina* although the early non-rectilinear growth of *reflua* and the reflexed apertural end of the tube in both *reflua* and *proboscis* are characters which have not apparently been reported for *Hyperammina* previously; Hofker (1972, p. 45)

stated that 'the tubular part [of *Hyperammina*] is nearly always straight'.

The somewhat contorted growth of *reflua* and *proboscis* is similar to that of the genus *Tolypammina* and *Ammovertella*, but as these are attached genera (see remarks under *Tolypammina*) then the two species (*reflua* and *proboscis*) cannot be placed therein.

The apparently flexible nature of the tubular section in these two species is reminiscent of the genus *Pelosina* but the test shape, proportions of proloculum to tubular section and the wall structure and composition all preclude placement in that genus. The genus *Saccorhiza* often shows irregular growth (Hofker 1972) but that genus also has sponge spicules characteristically in the wall of the test and has a bifurcating tubular chamber, neither of which characters are present in *reflua* or *proboscis*.

Derivation of name. *reflua* (L.): flowing back; referring to the proximal shape of the test.

Hyperammina proboscis n.sp.

Fig. 7A, B

Description. Test free; large; ellipsoidal proloculum, followed by a long second chamber which tapers directly from the proloculum without any constriction at the proloculum; apertural end of the tube reflexed for about one-third of its length; aperture a simple opening at the end of tube; test made of small angular sand grains with little cement, surface roughly finished.

Holotype. NMV P126964, from Gelantipy Road, Buchan, Buchan Caves Limestone, sample Ma 13.

Measurements (in mm)	diam. proloculum	tube diam.	length
Holotype NMV P126964	0.3	0.22	1.0
Paratype NMV P199414−ORCQ	0.16	0.12	0.56
Paratype NMV P199415−Ma 13	0.2	0.13	−

Distribution. Ma 13, ORCQ 10–15; *perbonus–inversus* zones.

Fig. 6. A–C, *Cylindramnina stolonifera* Bell n.sp. A, Paratype, NMV P199402, ×34, SALC 7. B, Holotype, NMV P126994, ×36, SALC 7. C, Paratype, NMV P199404, ×36, SALC 9. D–E, *Saccorhiza surculus* Bell n.sp. D, Holotype, NMV P126962, ×180, ORCQ 10–15. E, Paratype, NMV P199411, ×180, ORCQ 10–15. F, *Rhabdamnina proavita* Bell n.sp. holotype, NMV P126961, ×54, OTRC 7. G–1, *Rhabdammina linearis* Brady. G, NMV P199405, ×59, Ma 13. H, NMV P199407, ×90, BON 13.5–15. 1, NMV P126960, ×54, SALC 7. J, *Psammosphaera cava* Moreman, NMV P126965, ×200, OTRC 7. K, *Stegnammina cylindrica* Moreman, NMV P126967, ×135, OTRC 2. L–M, *Sorosphaera* sp. cf. *S. confusa* Brady. L, NMV P126966, ×108, OTRC 2. M, NMV P199418, ×180, OTRC 2. N, *Saccammina cumberlandiae* (Conkin), NMV P126982, ×144, BON 36–39. O, *Saccammina biosculata* Moreman, NMV P126968, ×180, ORCQ 10–15.

Remarks. H. proboscis differs from *H. reflua* in its ellipsoidal proloculum, no constriction at the base of the tubular chamber and in its rough surface. (See also remarks under *H. reflua*.)

Derivation of name. proboscis (L.): elephant trunk.

Hyperammina sp.

Fig. 7E

Description. Test consists of an inflated proloculum, ellipsiodal and slightly elongated followed by a tubular chamber constricted at junction with proloculum; diameter of tube about half that of proloculum; the tube is curved around the proloculum but separated from it; wall of fine particles with very few larger ones imbedded, surface fairly smoothly finished; aperture at end of tube.

Measurements (in mm)
Size: proloculum 0.2×0.14; diam. linear chamber 0.07.

Figured specimen. NMV P126955, Old Taravale Road cutting, Buchan, sample OTRC 7; Taravale Formation.

Distribution. OTRC 7; *perbonus* Zone.

Remarks. This species differs from both *H. reflua* and *H. proboscis* in the shape and size of the proloculum and the immediately recurved tubular chamber. The maximum size to which it may have grown is not known as all of the several specimens found only have a short tubular chamber as shown in Fig. 7E.

Family SACCAMMINIDAE Brady, 1884

Genus Psammosphaera Schulze, 1875

Psammosphaera cava Moreman, 1930

Fig. 6J

Psammosphaera cava Moreman 1930: 48, pl. 6, fig. 12.

Description. Test free; globular, small; test made from larger and smaller grains, but usually only of one type per test, grains in a single layer; surface slightly roughened but that made of the smaller grains smooth; no apparent aperture.

Figured specimen. NMV P126965, from Old Taravale Road cutting, Buchan, sample 7, Taravale Formation.

Measurement
Diameter 0.11 mm.

Distribution. OTRC 2, OTRC 7; *inversus-serotinus* zones.

Remarks. Specimens are smaller than those of Moreman but size does not seem to be an adequate specific differentiator for such a simple organism.

Genus Sorosphaera Brady, 1879

Sorosphaera sp. cf. S. confusa Brady, 1879

Fig. 6L, M

Description. Test globular to subglobular, with commonly one flattened side indicating a former attachment surface; test formed of very fine grains, well cemented and with the test wall smoothly finished inside and out; no apparent aperture.

Figured specimen. NMV P126966, from Old Taravale Road cutting, Buchan, sample 2, Taravale Formation.

Measurements (in mm)
Figured specimen   NMV P126966
                                        diam. chamber 1: 0.13
                                                 chamber 2: 0.12
Unfigured specimen NMV P199416−OTRC 2: 0.14
Unfigured specimen NMV P199417−OTRC 7: 0.16
Figured specimen   NMV P199418−OTRC 2
                                                 chamber 1: 0.11
                                                 chamber 2: 0.12

Distribution. OTRC 2, OTRC 5, OTRC 7; *inversus-serotinus* zones.

Remarks. The determination of species within *Sorosphaera* is difficult. The number of chambers

---

Fig. 7. A–B, Hyperammina proboscis Bell n.sp. A, Paratype, NMV P199414, ×90, ORCQ 10–15. B, Holotype, NMV P126964, ×45, Ma 13. C–D, *Hyperammina reflua* Bell n.sp., holotype, NMV P126963, ×54, ORCQ 10–15. D, Paratype, NMV P199412, ×54, ORCQ 10–15. E, *Hyperammina* sp., NMV P126955, ×144, OTRC 7. F, *Lagenammina stilla* Moreman, NMV P126970, ×90, Ma 13. G–1, *Lagenammina talenti* Bell n.sp. G, Holotype, NMV P126971, ×90, SALC 7. H, Paratype, NMV P199419, ×54, SALC 7. 1, Paratype, NMV P199420, ×63, ORCQ 10–15. J, L, *Lagenammina sphaerica* Moreman. J, NMV P126975, ×72, ORCQ 10–15. L, NMV P126969, ×59, Ma 13. K, M–N, *Lagenammina laxacolla* Bell n.sp. K, Holotype, NMV P126972, ×45, Ma 13. M, Paratype, NMV P199423, ×72, SALC 7. N, Paratype, NMV P199422, ×117, SALC 9. O–P, *Lagenammina ovata* Bell n.sp. O, Holotype, NMV P126973, ×54, SALC 9. P, Paratype, NMV P199426, ×90, ORCQ 10–15.

joined together has, in the past, been a character used to distinguish separate species (Dunn 1942; McClellan 1966) even though McClellan (1966) considered that it was highly likely that several species were only various chamber combinations of the one species. Single chambers only were quite common and rare double chamber forms occurred with one three chambered fragment recovered. These are considered to be aspects of the one species. In multichambered forms each test was complete i.e. there was a double wall between the adjacent chambers with no apparent openings between the chambers. The chambers are apparently not tightly attached together and the flattened side represented the adpressed surface. There was no apparent aperture; the various openings in the test wall were most likely due to dissolution effects during the acid treatment.

Single chambered specimens of *Sorosphaera* are distinguished from *Psammosphaera* in having a much thinner test wall and, in the studied specimens, in having one or more flattened surfaces.

Sorosphaera confusa has a many chambered agglomerated form (Brady 1879). No such shape was found in this study, but as the individual chambers show no apparent differences to those of *confusa*, the present material is placed in comparison with it.

Genus **Stegnammina** Morman, 1930

Stegnammina cylindrica Moreman, 1930

Fig. 6K

Stegnammina cylindrica Moreman 1930: 49, pl. 7, fig. 12.

Description. Test apparently free; cylindrical, ends slightly rounded; fine grained test with a smooth inner surface and a slightly roughened outside; no apparent aperture.

Figured specimen. NMV P126967, from Old Taravale Road cutting, Buchan, sample 2, Taravale Formation.

Distribution. OTRC 2; *serotinus* Zone.

Remarks. Some rarer specimens show an almost triangular cross-section rather than the round section of the commoner form; they are thus similar to *S. triangularis* Moreman but are not here considered as a separate species as the shape difference may be a deformation due to preservation.

Genus **Saccammina** Carpenter, 1869

Saccammina biosculata Moreman, 1933

Fig. 6O

Saccammina biosculata Moreman 1933: 395, pl. 47, fig. 6.

Description. test free; small; main chamber flattened but originally probably spherical; neck short, squat; wall thin, composed of fine sand grains with little cement, surface roughly finished; the neck is divided into two smaller necks for most of its length, these being almost perpendicular to each other; a simple aperture at the end of each neck.

Figured specimen. NMV P126968, from Old Rocky Camp Quarry, Buchan, sample ORCQ 10-15, Buchan Caves Limestone.

Measurements (in mm)
Figured specimen   NMV P126968   length: 0.17
                                                         width: 0.12

Distribution. ORCQ 10-15; *perbonus* Zone.

Remarks. Only one specimen was found but, although slightly smaller than Moreman's figured type, it does not differ in any other aspect. Moreman's specimen came from Middle Silurian sediments.

Saccammina cumberlandiae (Conkin, 1961)

Fig. 6N

Proteonina cumberlandiae Conkin 1961: 248–250, pl. 14, figs 1–3; pl. 26, figs 4–5; text-figs 2–3. — Conkin et al. 1963: 222, pl. 1, figs 12–14. — Conkin & Conkin 1964a: 32, pl. 2, figs 38–41.

Description. Test free, consisting of one inflated, slightly tapering chamber with a short, wide, tapering neck; aperture circular at end of neck; wall composed of medium-sized quartz grains fairly smoothly finished.

Figured specimen. NMV P126982, from Bonanza Gully, Bindi, sample BON 36-39, Buchan Caves Limestone.

Measurements (in mm)
Length 0.28; max. diam. 0.23; chamber length 0.23; neck length 0.05; neck max. diam. 0.11; neck min. diam. 0.05; length/width 1.23.

Distribution. From BON 36–39 only; *perbonus* Zone.

Remarks. Only rare specimens of this form were recovered. They compare closely with the description of *S. cumberlandiae* from the Lower Carboniferous (Lower Mississippian) of the U.S.A, although being somewhat more rounded

(l/w = 1.23) but this ratio is quite variable (Conkin et al. 1963; Conkin & Conkin 1964a; range 1.19–1.94).

Genus **Lagenammina** Rhumbler, 1911

Lagenammina sphaerica Moreman, 1930

Fig. 7J, L

Lagenammina sphaerica Moreman 1930: 51, pl. 5, fig. 15.

Description. Test free; a globular chamber with a long, narrow neck; aperture a simple opening at the end of the neck; test formed of fine grains with a fairly smoothly finished surface.

Figured specimens. NMV P126969, from Ma 13, Gelantipy Road, Buchan; Taravale Formation.
   NMV P126975, from from Old Rocky Camp Quarry, Buchan, sample ORCQ 10–15 m above the Murrindal Limestone, Taravale Formation; cast.

Measurements (in mm)
Figured specimen   NMV P126969   length: 0.16
                                                            width: 0.44
                                                      aperture: 0.06

Distribution. Ma 13, SALC 7, SALC 9, BON 13.5–15; *perbonus–inversus* zones.

Remarks. Due to compression during preservation most specimens were somewhat flattened but the degree of distortion was quite variable even within the one sample. Specimens from ORCQ 10–15 were preserved as casts and show the spherical shape without compression. The neck was often slightly curved, and its diameter varied between localities but, until more and better preserved specimens are found, these are not considered to be of sufficient importance to differentiate species.

Lagenammina stilla Moreman, 1930

Fig. 7F

Lagenammina stilla Morman 1930: 51, pl. 6, fig. 6.

Description. Test free; small; a globular chamber with a very short neck, about one-sixth the length of the globular test; thin walled, about two grains thick; test formed of a mixture of large and small sand grains, surface rough; aperture circular at end of short neck.

Figured specimen. NMV P126970, from Ma 13, Gelantipy Road, Buchan; Taravale Formation.

Measurements (in mm)
Figured specimen   NMV P126970   length: 0.3
                                                            width: 0.24
                                                      aperture: 0.04

Distribution. Ma 13; *inversus* Zone.

Remarks. The test is made of a random placement of small and larger sand grains apparently with little cement, giving the test a rough external surface. The interior of the test is smooth suggesting that originally there was an inner organic layer on which the grains were laid.

Lagenammina talenti n.sp.

Fig. 7G–I

Description. Test free; small; ellipsoidal body chamber followed by a long, wide, slightly curving neck; test wall formed of largish grains, surface rough; aperture circular at end of neck.

Holotype. NMV P126971, from south arm, Limestone Creek, Bindi, sample 7, Taravale formation.

Measurements (in mm)	length	width	aperture
Holotype NMV P126971	0.5	0.2	0.05
Paratype NMV P199419 – SALC 7	0.8	0.26	0.06
Paratype NMV P199420 – ORCQ	0.48	0.26	0.09
Paratype NMV P199421 – Ma 13	0.51	0.27	0.07

Distribution. SALC 7, Ma 13, ORCQ 10–15; *perbonus–inversus* zones.

Remarks. The body chamber is usually compressed. The long neck shows different degrees of curvature which suggests that it may have been flexible when living. The overall shape of this species clearly separates it from other *Lagenammina*. *L. silnica* Malic 1992 has a similar body chamber shape but is a much smaller species and lacks the long, produced neck of *L. talenti*.

Derivation of name. For Professor J. A. Talent, Macquarie University, for his contributions to the biostratigraphy of the Devonian in Australia.

Lagenammina laxacolla n.sp.

Figs 7K, M, N; 8A

Description. Test free; small; a discoidal chamber with a short, straight, wide neck; test formed of fine grains, smoothly finished; aperture circular at end of neck.

Holotype. NMV P126972, from Gelantipy Road, Buchan, sample Ma 13, Buchan Caves Limestone.

Measurements (in mm)	length	width	aperture
Holotype NMV P126972	0.5	0.48	0.1
Paratype NMV P199422 – SALC 9	0.32	0.28	0.05
Paratype NMV P199423 – SALC 7	0.53	0.42	0.06
Paratype NMV P199424 – Ma 13	0.48	0.32	0.06
Paratype NMV P199425 – BON 36–39	0.48	0.26	0.07

Distribution. Ma 13, SALC 7, SALC 9, BON 36–39; *perbonus-inversus* zones.

Remarks. This small species differs from *L. stilla* in having a short, wide neck.

Some specimens from Bonanza Gully and Gelantipy Road differ in having an aboral spine present (Fig. 8A). Whether this is a sufficient character for specific difference must await better preserved specimens.

Derivation of name. laxus (L.): wide; *collum* (L.): neck.

Lagenammina ovata n.sp.

Fig. 7O, P

Description. Test free; large ovate body chamber, with a short, narrow neck; test made of small uniform grains with little cement, surface slightly rough; aperture circular at end of neck.

Holotype. NMV P126973, from south arm, Limestone Creek, Bindi, sample 9, Taravale Formation.

Measurements (in mm)	length	width	aperture
Holotype NMV P126973	0.74	0.38	0.06
Paratype NMV P199426–ORCQ	0.48	0.36	0.07

Distribution. SALC 9, ORCQ 10–15; *perbonus-inversus* zones.

Remarks. L. ovata differs from the other species of *Lagenammina* in its large ovate body chamber and short narrow neck. It seems closest to *L. talenti* from which it differs in body/neck proportions and in the smoother test surface.

Derivation of name. ovata (L.): oval-shaped.

Genus **Stomasphaera** Mound, 1961 *emend.* Bell (in Simpson et al. 1993)

Stomasphaera cyclops n.sp.

Fig. 9A–D

Description. Test free; subglobular to ovate chambers joined to form a linear to arcuate series; chamber size variable but not necessarily increasing in size along the series; test wall coarsely agglutinate with a smooth to rough surface; aperture rounded to elongate, may be depressed slightly and is surrounded by an area of finer grains.

Holotype. NMV P126977, from Bonanza Gully, Bindi, sample 220–240. Buchan Caves Limestone.

Measurements (in mm) (largest chamber only measured)	length	width	aperture
Holotype NMV P126977	0.35	0.23	0.09 × 0.06
Paratype NMV P199432 –BON 220–240	0.4	–	0.08
Paratype NMV P199433 –BON 220–240	0.4	–	0.12

Distribution. Known from the type locality only, BON 220–240; *perbonus* Zone.

Remarks. S. cyclops differs from the Victorian Upper Silurian form *S. globosa* Bell (*in* Simpson et al. 1993) in having a larger aperture, in the chamber shape being not as globular but more elongate and in the wide band of finer grains about the aperture. The aperture remains open in earlier chambers. There is apparently no connection between successive chambers. Both single and multithalamous tests were present.

The genus *Stomasphaera* differs from *Saccamminoides* Geroch, 1955 which shows a sharp change in direction of coiling after the first 2–3 chambers (Loeblich & Tappan 1988). This coiling character has been not seen in any specimens of *cyclops* or *globosa*.

Derivation of name. cyclops (L.): a race of one-eyed giants; referring to the large aperture.

Genus **Ordovicina** Eisenack, 1937

Ordovicina eisenacki (Conkin & Conkin, 1964)

Fig. 8I–K

Amphitremoida eisenacki Conkin & Conkin 1964b: 73, pl. 12, figs 8–10.

Fig. 8. A, *Lagenammina laxacolla* Bell n.sp., paratype, NMV P199424, ×90, Ma 13, note abapertural spine. B–C, *Pelosina grandaeva* Bell n.sp. B, Holotype, NMV P126976, ×135, ORCQ 10–15. C, Paratype, NMV P126999, ×59, Ma 13. D–E, *Thurammina echinata* Dunn. E, NMV P126978, ×72, BON 36–39. D, NMV P, ×90, OTRC 7. F, *Thurammina foesteri* Dunn, NMV P126981, ×72, ORCQ 10–15. G, *Thurammina subsphaerica* Moreman, NMV P126979, ×72, BON 13.5–15. H, *Thurammina tributa* Dunn, NMV P126980, ×108, BON 39–44. I–K, *Ordovicina eisenacki* (Conkin & Conkin). I, NMV P127000, ×72, BON 36–39. J, NMV P127001, ×126, BON 13.5–15. K, NMV P199434, ×135, ORCQ 10–15. L–M, *Patellammina prona* Bell n.sp. L, Holotype, NMV P126985, ×54, BON 220–240. M, Paratype, NMV P126998, ×63, BON 220–240. N, *Hemisphaerammina* sp., NMV P199599, ×126, OTRC 7.

Description. Test free; a single fusiform chamber with a small aperture at each end; the apertural ends slightly produced; test composed of fine sand grains, slightly roughly finished; the surface of the test shows transverse low ridges.

Measurements (in mm)	length	width	apertures	
Figured specimens			S_1	S_2
NMV P199434 – ORCQ	0.36	0.2	0.03	0.02
NMV P127001 – BON 13.5-15	0.36	0.12	0.03	broken
NMV P127000 – BON 36-39	0.6	0.35	0.09	0.05

Distribution. BON 13.5-15, BON 36-39, ORCQ 10-15; *perbonus* Zone.

Remarks. The specimens recovered were larger than those described by Conkin & Conkin (1964b) but appear otherwise to be the same species. All specimens were compressed and the surface transverse ridges may be an artefact of the preservation. The apertural ends were deformed and the measurements given are lower values only.

The present specimens differ from the larger form recorded by Conkin & Conkin (1964b) as *Amphitremoida* sp. in lacking the 'collar' surrounding the apertures, and from *A. hauffmani* (Conkin & Conkin 1964b) in their much larger size and different length/width ratios. *O. kielcensis* (Malec 1992) described from the upper Emsian beds of the Gory Swietokrzyskie Mountains of Poland is similar to *O. eisenacki* but appears from the data given to be more slender; however the varying amounts of compaction (flattening) of specimens could easily account for the small differences between these two species.

Genus **Pelosina** Brady, 1879

Pelosina grandaeva, n.sp.

Fig. 8B, C

Description. Test free; a single fusiform chamber, about three times as long as wide, with long tubular extensions at either end; fine grained test wall but not smoothly finished; simple circular aperture at ends of the tubular extensions.

Holotype. NMV P126976, from Old Rocky Camp Quarry, Buchan, sample ORCQ 10-15, Taravale Formation.

Measurements (in mm)	length	width	aperture	
			S_1	S_2
Holotype NMV P126976	0.38	0.06	0.02	0.02
Paratype NMV P126999 – Ma 13	0.64	0.22	0.05	broken

Distribution. ORCQ 10-15, Ma 13; *perbonus-inversus* zones.

Remarks. The tubular extensions were of unequal length in the type specimen but this is due likely to breakages during preservation as other specimens were of more equal length. The produced ends appear to have been flexible since they are slightly curved.

Pelosina was previously known to range from the Cretaceous to Recent (Loeblich & Tappan 1988).

Derivation of name. grandaeva (L.): very old.

Genus **Thurammina** Brady, 1879

Thurammina echinata Dunn, 1942

Fig. 8D, E

Thurammina echinata Dunn 1942: 331, pl. 42, figs 20, 21, 23.

Description. Test free; globular, with many short, pointed papillae on the surface; papillae are hollow with a simple opening at the end of each; test composed of very fine sand grains, smoothly finished.

Figured specimen. NMV P126978, Bonanza Gully, Bindi, sample 36-39, Buchan Caves Limestone.

Measurement (in mm)	
Figured specimen NMV P126978	diameter: 0.48

Distribution. ORCQ 10-15, BON 36-39, OTRC 5, OTRC 7; *dehiscens-perbonus* zones.

Remarks. A widespread and common species. The test is thin and often distorted or compressed but without showing any signs of breakages

Fig. 9. A–D, *Stomasphaera cyclops* Bell n.sp. A, Holotype, NMV P126977, ×72, BON 220-240. B, Close-up of aperture of holotype, ×180. C, Paratype, NMV P199432, ×54, BON 220-240. D, Close-up of aperture of paratype, ×180. E, *Metamorphina tholus* (Moreman), NMV P126984, ×72, BON 13.5-15. F, *Thurammina zaramama* Bell n.sp., holotype, NMV P126974, ×72, Ma 13. G, *Reophax troca* Bell n.sp., holotype, NMV P126993, ×126, OTRC 7. H, *Lituotuba torquata* Bell n.sp., holotype, NMV P126990, ×126, OTRC 7. 1, *Lituotuba helix* Bell n.sp., holotype, NMV P126991, ×72, OTRC 5. J, *Hormosina divitiae* Bell n.sp., holotype, NMV P126992, ×72, BON 220-240. K-M, *Kerionammina prolata* Bell n.sp. K, Holotype, NMV P126986, ×117, ORCQ 10-15. L, Paratype, NMV P199597, ×180, ORCQ 10-15, showing internal longitudinal walls. M, Close-up of paratype, arrows indicating transverse partitions between longitudinal walls, ×540.

indicating that the test may have been flexible when the animal was alive.

Thurammina subsphaerica Moreman, 1930

Fig. 8G

Thurammina subsphaerica Moreman 1930: 52, pl. 5, fig. 16.

Description. Test free; globular; a small number (about 20) of short papillae more or less evenly distributed over the surface; test with a thin wall of very fine grains with little cement, surface smooth; simple circular aperture at the end of each papilla.

Figured specimen. NMV P126979, from Bonanza Gully, Bindi, sample 13.5–15, Buchan Caves Limestone.

Measurement (in mm)
Figured specimen NMV P126979   diameter: 0.53

Distribution. BON 13.5–15, OTRC 5, OTRC 7, ORCQ 10–15; *dehiscens–perbonus* zones.

Remarks. *T. subsphaerica* differs from *T. echinata* in the fewer but broader and less pointed papillae. As with *echinata*, *subsphaerica* was possibly flexible when alive.

Thurammina tributa Dunn, 1942

Fig. 8H

Thurammina tributa Dunn 1942: 334, pl. 43, fig. 20 (as *T. trituba*).

Description. Test free; small; globular to ellipsoidal; three papillae, short, wide, more or less evenly positioned on the equatorial plane of the globular chamber; test formed of medium sized sand grains with little cement; aperture a simple opening at the end of each papillae.

Figured specimen. NMV P126980, from Bonanza Gully, Bindi, sample 39–44, Buchan Caves Limestone.

Measurements (in mm)
Figured specimen NMV P126980
    maximum diameter: 0.28; minimum diameter: 0.21

Distribution. BON 39–44, BON 56–60.5; *perbonus* Zone.

Remarks. The three short, evenly placed papillae make this species easily identifable.

Thurammina foerstei Dunn, 1942

Fig. 8F

Thurammina foerstei Dunn 1942: 331, pl. 43, fig. 27.

Description. Test free; globular, with two low, dome-shaped papillae almost diametrically opposed; test made from even sized, very small grains, smoothly finished; aperture a simple opening at the summit of each papilla.

Figured specimen. NMV P126981, from from Old Rocky Camp Quarry, Buchan, sample ORCQ 10–15.

Measurement (in mm)
Figured specimen NMV P126981   diameter: 0.39

Distribution. ORCQ 10–15; *perbonus* Zone.

Remarks. My specimens are larger than Dunn's original (0.75 mm diameter against 0.29 mm), but otherwise there are no apparent differences.

Thurammina zaramama, n.sp.

Fig. 9F

Description. Test free; ellipsoidal chamber, covered with many (± 100) small, short papillae arranged in rows; test wall thin, very finely agglutinated; interior surface smooth; aperture a small opening at the top of most papillae; specimens were usually red-brown.

Holotype. NMV P126974, from Gelantipy Road, Buchan, sample Ma 13, Buchan Caves Limestone.

Measurements (in mm)
Holotype NMV P126974   length: 0.6; width: 0.23.

Distribution. Ma 13; BON 60.5–65; *perbonus–inversus* zones.

Remarks. The shape of the test and the large number of papillae are sufficient to distinguish this species from any other *Thurammina*. The shape of the chamber varied with the locality; those from Gelantipy Road had a long ellipsoidal form whilst those from Bonanza Gully were more rounded. Whether this is a reflection of the differing sedimentary facies or an age difference must await more specimens from other localities.

Derivation of name. *zaramama* (?Quechua, Peruvian native): for the similarity to the stone imitation maize heads of the Andean Indians (Whymper 1892).

Genus Webbinelloidea Stewart and Lampe, 1947

Webbinelloidea crassus, n.sp.

Fig. 10J, K

Description. Test attached; in the form of a low dome with a circular attachment area; test made

of coarse grains, wall thick, but variable depending on the size of the grains used, surface rough; internal surface smooth; no apparent aperture.

Holotype. NMV P126983; from Bonanza Gully, Bindi, sample 206, Buchan Caves Limestone.

Measurements (in mm)
maximum diameter: 0.325; aperture diameter: 0.1

Distribution. BON 206, BON 220–240; *perbonus* Zone.

Remarks. This a very robust *Webbinelloidea*, formed from very coarse sand grains. Only single-chambered forms were recovered although *Webbinelloidea* may show multichambered tests (Stewart & Lampe 1947).

Genus **Metamorphina** Browne, 1963

Metamorphina tholus (Moreman, 1933)

Fig. 9E

Webbinella tholus Moreman 1933: 395, pl. 47, figs 8, 10.
Metamorphina tholus – McClellan 1966: 489, pl. 37, figs 15–19; pl. 41, figs 15–19.

Description. Test probably formerly attached; a low dome, sometimes showing a marginal flange; monothalamous but individual chambers may aggregate into pseudomultilocular tests; sutures between chambers straight; wall of fine grains, smooth surface; no apparent aperture.

Figured specimen. NMV P126984, from Bonanza Gully, Bindi, sample 13.5–15, Buchan Caves Limestone.

Measurement (in mm)
Figured specimen NMV P126984
chamber diameter: 0.22

Distribution. BON 13.5–15; *perbonus* Zone.

Remarks. The low-domed test and the absence of a basal wall serve to place the specimens in the genus *Metamorphina*. McClellan (1966) has given a full discussion of the criteria for distinguishing *Metamorphina* Browne 1963, *Webbinelloidea* Stewart & Lampe 1947 and *Hemisphaerammina* Loeblich & Tappan 1957.

Although the figure shows a four-chambered specimen, single and double chambered forms were more common.

Genus Hemisphaerammina
Loeblich & Tappan, 1957

Hemisphaerammina sp.

Fig. 8N

Description. Test hemispherical, with a thick wall; attachment surface flat, smooth with no flanges and no evidence of a basal membrane; wall coarse and roughly finished.

Figured specimen. NMV P; Old Taravale Road cutting, Buchan, sample 7, Taravale Formation.

Distribution. OTRC 7; *perbonus* Zone.

Remarks. Only rare specimens were recovered. It should be noted that the possibility exists that some specimens placed within the genus *Hemisphaerammina* may not belong within the Foraminiferida but represent egg-capsules of different species of gastropods (Adegoke et al. 1969; Bell & Burn 1979).

Genus **Patellammina** n.gen.

Genotype. *Patellammina prona* n.sp.; NMV P126985, from Bonanza Gully, Bindi, sample BON 220–240, Buchan Caves Limestone.

Description. Test apparently free; multilocular, upto three chambers joined in an irregular series; chambers are flattened, disc-like, with a floor; in section the chambers are meniscus-shaped; aperture an irregular hole, usually subcircular, in the concave (?basal) face; test coarsely agglutinated, with a rough surface.

Remarks. This genus belongs in the Hemisphaerammininae as it has obvious affinities with *Hemisphaerammina*, *Webbinelloidea*, *Colonammina* and *Ammopemphix*. *Patellammina* n.gen. differs from *Hemisphaerammina* and *Webbinelloidea* in being very flattened and not hemispherical, and from *Hemisphaerammina* and *Colonammina* in the occurrence of not only single chambered but multiple chambered tests; *Colonammina* and *Ammopemphix* have the aperture on the upper, convex surface. It differs from the Recent genus *Causia* Rhumbler which has a chitinous test with only a few attached sand grains and which also possesses a peripheral flange.

It is considered that *Patellammina* n.gen. was free living as no attached specimens have been found nor is there any evidence of attachment scars on any specimens.

Derivation of name. patella (L.): dish, saucer-shaped.

Patellammina prona n.sp.

Fig. 8L, M

Description. As for the genus *Patellammina*.

Holotype. NMV P126985, from Bonanza Gully, Bindi, sample 220–240, Buchan Caves Limestone.

Measurements (in mm)		chamber diam.	aperture
Holotype NMV P126985		0.6	0.07
Paratype NMV P126998			
—BON 220–240	chamber 1:	0.34	0.17
	chamber 2:	0.34	0.1
Paratype NMV P126997			
—BON 220–240		0.31	0.1
Paratype NMV P126996—Ma 13		0.31	0.09

Distribution. BON 220–240, Ma 13; *perbonus-inversus* zones.

Remarks. As for the genus.

Derivation of name. prona (L.): flatlying.

Genus Kerionammina Moreman, 1933

Kerionammina prolata n.sp.

Fig. 9K–M

Description. Test attached; flattened and spreading in a digitate manner, with once bifurcating arms; early chambers indistinct; wall thin, finely arenaceous — on the upper, unattached side with a roughened surface with transverse ridges, and the attached surface smooth, often translucent to transparent; interior divided into chamberlets which run out to the tips of the arms, the wall between the chamberlets is thin and smooth; aperture not observed.

Holotype. NMV P126986, from Old Rocky Camp Quarry, Buchan, sample 10–15, Taravale Formation.

Measurements (in mm)	basal width	width	length
Holotype NMV P126986	0.35	arm 1: 0.05	0.2
		arm 2: 0.04	0.1
		arm 3: 0.04	—

Paratype NMV P199597
distance between longitudinal partitions:
0.008–0.012
distance between transverse internal partitions:
0.006–0.01

Distribution. ORCQ 10–15, OTRC 7; *perbonus-inversus* zones.

Remarks. The test shows no obvious places of attachment but the varying shapes of the specimens indicate that they were supported during growth and conformed to the shape of the supporting body.

The interior chamberlets, in wider specimens, are arranged in parallel rows but, in narrow specimens and in the narrower arms, the chamber-lets are often irregularly placed. Moreman (1933) erected the genus for specimens from the Middle Ordovician.

Kerionammina prolata n.sp., differs from *K. favus* Moreman in having a more regular, digitate spreading pattern, in being finely arenaceous and in having no apparent apertures.

The Recent genus *Jullienella* Schlumberger has some features similar to *Kerionammina* (rigid agglutinated walls, flabelliform shape, digitate growth, interior with weak to strong transverse ridges). However Norvang (1961) did not consider *Jullienella* to possess even rudimentary chamberlets as the internal partitions are short and widely scattered, although Buchanan (1960) stated that the internal space was divided into 'intercommunicating canals by longitudinal partitions of cemented sand grains' and Hayward & Gordon (1984) in describing a new species of *Jullienella* from New Zealand stated that the interior surface of the walls was weakly wrinkled. The possibility exists that *Kerionammina* in the Palaeozoic is the ancestor of the Recent *Jullienella* by a change in the form of the interlaminary space but the material available at present does not permit further discussion of this point.

Conkin & Conkin (1982) assigned *K. favus* to Incertae sedis without giving any reasons.

Derivation of name. prolata (L.): extended.

Family AMMODISCIDAE Reuss, 1862

Subfamily Tolypammininae Cushman, 1928

The identification of the vermiform Lower Palaeozoic foraminiferal genera has caused much confusion and discussion in the literature. In particular the separation of the genera *Tolypammina* Rhumbler 1895 and *Ammovertella* Cushman 1928 has given rise to much discussion and varying interpretations of these genera (Barnard 1958; Bermudez & Rivero 1963; Conkin 1961; Conkin & Conkin 1964b; Gutschick & Treckman 1959; Henbest 1963; Hofker 1972; Ireland 1956).

In an attempt to distinguish these two genera Ireland (1956) proposed that the main distinguishing features were the tube cross-section, coiling or bending in the initial growth stage and the presence or absence of an agglutinate floor to the tubular section wherever it was attached. However he included in his description of the species within each genus forms with and without these characteristic features. Gutschick & Treckman (1959) in their study of Lower Carboniferous foraminiferans followed Ireland but found

(p. 241) '... some tolypamminids contradict some of Ireland's criteria for distinguishing between *Tolypammina* and *Ammovertella*'.

Barnard (1958) proposed a simple division of the genera: *Tolypammina* having no initial coiling about the proloculum, and *Ammovertella* with a planispiral initial coiling of the tubular section about the proloculum. He also pointed out that 'In both *Tolypammina* and *Ammovertella* the final tubular portion of the test is similar and without study of the initial part it is impossible to separate the genera' (Barnard 1958: 117).

Conkin (1961) proposed a separation of the genera based on the second chamber; his criteria are similar to those of Ireland.

A third genus of Palaeozoic tolypamminid, *Minammodytes*, was introduced by Henbest (1963), which differed from *Tolypammina* in having the second chamber partly enclosing the proloculum and from *Ammovertella* in not having the second chamber growing in a zigzag manner. However this latter difference would seem to be, at most, only a specific distinguishing character.

Henbest (1963) considered *Minammodytes* to be an early Carboniferous genus, while Conkin & Conkin (1982), in a review of the Palaeozoic North American foraminiferans, placed the first appearance of *Ammovertella* as Lower Carboniferous and of *Tolypammina* as Middle Ordovician, but made no mention of *Minammodytes*.

As the degree of attachment of the second chamber and so the presence or absence of a 'floor' are both greatly variable within specimens that otherwise appear identical and the degree of diagensis of the sediments causes varying amounts of distortion of the tests, the simplest criterion for separating *Tolypammina* and *Ammovertella* is that proposed by Barnard (1958) and is followed here. *Minammodytes* is considered a junior synonym of *Serpulopsis* Girty 1911 (Loeblich & Tappan 1988).

The Upper Carboniferous *Ammodiscella* Ireland 1956 and the Recent *Hemidiscella* Bock 1968 both differ from *Tolypammina* and *Ammovertella* in having a symmetrical planispirally enrolled second chamber before the coiling becomes irregular.

Genus **Tolypammina** Rhumbler, 1895

Tolypammina anguinea n.sp.

Fig. 10A, B

Tolypammina sp.—Bell in Simpson et al. 1993: 146, figs 3L, M.

Description. Test originally attached; subspherical proloculum followed by a long hemitubular second chamber which usually winds about in a highly irregular manner; wall formed of fine grains, surface fairly rough; aperture circular at the end of the second chamber; attached side of test shows no evidence of a floor of attachment but the edges of the tube may be slightly flared.

Holotype. NMV P126988, from ORCQ 10–15, Old Rocky Camp Quarry, Buchan, Buchan Caves Limestone.

Measurements (in mm)	proloculum diam.	aperture
Holotype NMV P126988	0.02	0.03
Paratype NMV P199427–ORCQ	0.03	0.06
Paratype NMV P199428–BON 36–39	0.06	0.12

Distribution. OTRC 5, OTRC 7, Ma 13, BON 13.5–15, BON 29–35, BON 36–39, ORCQ 10–15; *dehiscens-inversus* zones; also known from the Upper Silurian (Ludlow) of Eastern Victoria (Simpson et al. 1993).

Remarks. This species is very similar to *T. nexuosa* Crespin from the Australian Upper Devonian but differs in having a rough unpolished surface. It appears closest to *T. bransoni* Conkin et al. 1968 from the Mississippian of Missouri but differs in showing little or no evidence for a basal floor. As is usual with many of the tolypamminids the shape of the second chamber is highly variable. Kazmierczak (1973) found *Tolypammina* to live within the water channels of sponges and so the constrictions on its mode of growth cause the great variability in morphology shown by this genus. Apart from very rare *Receptaculites* no sponges are known from the Buchan Caves Limestone or Taravale Formation.

Derivation of name. anguinea (L.): snaky.

Tolypammina tantula n. sp.

Fig. 10C–E

Description. Test free; a long cylindrical tube which expands from a small, egg-shaped proloculum; chamber walls usually entire, made of coarse grains, roughly finished; aperture at end of tube.

Holotype. NMV P126995; from Bonanza Gully, Bindi, sample BON 13.5–15, Buchan Caves Limestone.

Measurements (in mm)	proloculum diam.	aperture
Holotype NMV P126995	0.036	0.1
Paratype NMV P199903–BON 29–35	0.07	0.09

Distribution. BON 13.5–15, BON 29–35, BON 36–39; OTRC 5, OTRC 7; *perbonus* Zone.

Remarks. This is a more robust species than *T. anguinea* n.sp. from which it differs in having a completely tubular second chamber with no apparent indication of attachment to a substrate, in the normally non-meandering habit of growth and in the tiny proloculum. Specimens with a proloculum are rare; the early part of the test is thin and fragile compared to the later more robust section.

Derivation of name. tantula (L.): so small; referring to the proloculum and initial part of test.

Genus **Ammovertella** Cushman, 1928

Ammovertella calyx n.sp.

Figs 4, 10F–I

Description. Test originally attached; small; hemispherical to hemiellipsoidal proloculum followed by a hemitubular second chamber which encircles the proloculum for about three-quarters of a turn, and then becomes sinuous and ultimately rectilinear; test wall made of small sand grains, several grains in thickness, coarsely finished outside but the interior surface smooth; the attached surface is flat, without any floor along its entire length; aperture is a simple tubular opening at the end of the second chamber.

Holotype. NMV P126989, from Bonanza Gully, Bindi, sample 13.5–15, Buchan Caves Limestone.

Measurements (in mm)

	proloculum diam.	length
Holotype NMV P126989	0.02	0.27
Paratype NMV P199429—BON 13.5–15	0.02	0.21
Paratype NMV P199430—BON 13.5–15	0.03	0.4

Distribution. BON 13.5–15, ORCQ 10–15; *perbonus* Zone.

Remarks. Because of the partly enrolled second chamber this species is placed in the genus *Ammovertella.* In some specimens there was a small flange on the wall edge at the attachment point. There was a large variation in the degree of coiling, the thickness of chamber walls, in the chamber diameter and, subsequently, in the shape of the test (Figs 4, 10F–I). Very rare specimens were found with a more enrolled early chamber development (Fig. 4E). These variations possibly only reflect the influence of the attachment surface and the surrounding environmental factors (Atkinson 1969).

Derivation of name. calyx (L.): limestone.

Genus **Lituotuba** Rhumbler 1895

Loeblich & Tappan (1988: 69) have stated, without giving reasons, that the Palaeozoic forms previously placed in *Lituotuba* are not congeneric with that genus. Until reasons for this change are given I have retained the genus for Early Devonian species from Victoria but have written it as '*Lituotuba*'.

'Lituotuba' torquata n.sp.

Fig. 9H

Description. Test free; early stage is a bulbous proloculum followed by an almost planispiral coiled undivided cylindrical tube of more or less one turn; in the later stage the tube becomes an uncoiled, undivided rectilinear segment with an helical twist of two (or more) turns imposed upon it; test wall fine grained, fairly smoothly finished; the aperture is a simple opening at the end of the linear segment.

Holotype. NMV P126990, from Old Taravale Road cutting, Buchan, sample 7, Taravale Formation.

Measurements (in mm)

	length	width	neck width
Holotype NMV P126990	0.43	0.26	0.08
Paratype NMV P199431 —BON13.5–15	0.4	0.22	0.08

Fig. 10. A–B, *Tolypammina anguinea* Bell n.sp. A, Holotype, NMV P126988, ×180, ORCQ 10–15, attached side view. B, Paratype, NMV P199427, ×72, ORCQ 10–15, dorsal view. C–E, *Tolypammina tantula* Bell n.sp. C, Paratype, NMV P199903, ×63, BON 29–35, attached surface view. D, Holotype, NMV P126995, ×54, BON 13.5–15, dorsal view. E, Paratype, NMV P199902, ×72, BON 13.5–15, dorsal view. F–I, *Ammovertella calyx* Bell n.sp. F, Holotype, NMV P126989, ×180, BON 13.5–15, attached surface view. G, Paratype, NMV P199429, ×90, BON 13.5–15, dorsal view. H, Paratype, NMV P199430, ×135, BON 13.5–15, attached surface view. I, Paratype, NMV P199901, ×270, BON 13.5–15, attached surface view, arrow indicates double wall. J–K, *Webbinelloidea crassus* Bell n.sp. J, Holotype, NMV P126983, ×110, BON 206, oblique view of attached surface. K, Paratype, NMV P199900, ×90, oblique view of attached surface, arrow indicates small attachment aperture. L. *Thuramminopsis sphaeroidalis* Plummer, NMV P126987, ×54, OTRC 7.·

Distribution. OTRC 7, BON 13.5–15; *dehiscens–perbonus* zones.

Remarks. The distinctive twisted neck easily distinguishes this species from other Palaeozoic '*Lituotuba*' spp. The degree of twisting is variable but is always present.

Derivation of name. *torquata* (L.): wearing a twisted collar.

'Lituotuba' helix n.sp.

Fig. 9I

Description. Test free; initially a small rounded proloculum followed by an unsegmented cylindrical tube of two and one half whorls helically arranged, then uncoiling and becoming rectilinear; test wall fine grained, surface smoothly finished; aperture a simple opening at the end of the tube.

Holotype: NMV P126991, from Old Taravale Road cutting, Buchan, sample 5, Taravale Formation.

Measurements (in mm)	length	width	aperture
Holotype NMV P126991	0.53	0.2	0.08

Distribution. Known from the type locality only, OTRC 5; *dehiscens* Zone.

Remarks. This species is readily distinguished by the early helix-form of the test.

Derivation of name. *helix* (L.): referring to the early whorl shape.

Family HORMOSINIDAE Haeckel, 1894

Genus **Hormosina** Brady, 1879

Hormosina divitiae n.sp.

Fig. 9J

Description. Test free; small; multilocular with oblate, thin-walled chambers gradually increasing in size, arranged rectilinearly; sutures constricted and well marked; wall finely agglutinate and smoothly finished; aperture terminal, rounded, on a slightly produced neck.

Holotype. NMV P126992, from Bonanza Gully, Bindi, sample 220–240, Buchan Caves Limestone.

Measurements (in mm)		length	width	aperture
Holotype NMV P126992	ch. 1:	0.11	0.22	
	ch. 2:	0.15	0.23	
	ch. 3:	0.18	0.23	0.09

Distribution. Known only from the type locality, BON 220–240; *perbonus* Zone.

Remarks. This species is placed in the genus *Hormosina* because of its rectilinear form, thin walled chambers and produced apertural neck, even though the chambers are not spherical which has been considered a diagnostic feature of *Hormosina* (Bronnimann & Whittaker, 1980). Previously *Hormosina* was only known to range from Jurassic to Recent (Loeblich & Tappan 1988).

Derivation of name. *divitiae* (L., f., pl.): riches, bonanza; referring to the locality, Bonanza Gully.

Genus **Reophax** Montfort, 1808
emend. Bronnimann and Whittaker, 1980

Reophax troca n.sp.

Fig. 9G

Description. Test free; small; multilocular, uniserial arrangement of chambers in a slightly arcuate chain; initial chamber fairly large, globular, with successive chambers slightly oblate, increasing in size; sutures clearly defined, slightly oblique; aperture terminal, rounded, on a very short wide neck; test formed of moderate sized grains, somewhat roughly finished.

Holotype. NMV P126993, from Old Taravale Road cutting, Buchan, sample 7, Taravale Formation.

Measurements (in mm)	length	width	aperture
Holotype NMV P126993	0.28	ch 1: 0.08	
		ch 2: 0.12	0.03

Distribution. Known from the type locality only, OTRC 7; *dehiscens* Zone.

Remarks. Because of the non-symmetrical chambers and their asymmetrical arrangement this species is placed in *Reophax* as emended by Bronnimann & Whittaker (1980) not in *Hormosina* notwithstanding the presence of a short terminal neck.

Although the genus *Reophax* is known from the Ordovician no previous Early Devonian specimens have been reported (Gutschick 1986) although microforaminiferal organic linings from the Pragian (*sulcatus* Zone) of New South Wales, Australia, have been referred to this genus (Winchester-Seeto & Bell 1994).

Derivation of name. *troca*: anagram of locality, Old Taravale Road cutting.

INCERTAE SEDIS

Genus **Thuramminoides** Plummer, 1945

Thuramminoides sphaeroidalis Plummer, 1945

Fig. 10

Thuramminoides sphaeroidalis Plummer 1945: 218, pl. 15, figs 4-10.

Figured specimen. NMV P126987, from OTRC 7, Old Taravale Road cutting, Buchan; Taravale Formation.

Measurement (in mm)
Figured specimen NMV P126987   diameter: 0.56

Distribution. dehiscens–serotinus zones.

Remarks. This species was very widespread and was found in many samples which contained no foraminiferans.

It was more common in the sandier samples from Old Taravale Road cutting (OTRC) and at south arm, Limestone Creek, Bindi, (SALC), but infrequent in the purer limestones of Bonanza Gully (BON) and Old Rocky Camp Quarry (ORCQ 10-15). Specimens were always compressed and often split.

Trochammina bursaria, which Chapman (1933) described from possible Lower Devonian mudstones near Mitcham, Victoria (registered specimen NMV P26009, Museum of Victoria Palaeontology Collection), is identical to forms placed here in *T. sphaeroidalis*; the supposed 'internal tubular chamber' of Chapman's species is just a compressional effect.

Although described by Plummer (1945) as a foraminiferan, this species has been remarked as having spore-like affinities (Conkin et al. 1965) and also has been referred to the radiolaria (Conkin et al. 1968; Conkin et al. 1981).

FACIES DEPENDENCE OF FAUNA

Whilst the distinction between the limestones and marly limestones facies is not clear cut due to the varying amounts of argillaceous material found in the calcareous sediments, the faunas can be broadly separated into species mainly characteristic of the limestones (28 spp.) and those of the more muddier sediments (2 spp.), whilst 15 spp. occurred in both facies (Table 2). The genera *Thurammina, Sorosphaera, Kerionammina, Saccammina, Patellammina, Hormosina, Ammovertella, Metamorphina, Ordovicina* and *Hemisphaerammina* were only found in the limestones. Of the other genera in the fauna, some species within each genus had a restricted facies distribution e.g. *Cystingarhiza* where three species were present in both facies but *C. mawsonae* was only found in the muddier phases, and *Hyperammina* where *H. reflua* was only present in the purer limestones but *H. proboscis* was present in both phases. *Lagenammina* spp. were found in both facies but predominately in the muddier phases; in present day seas *Lagenammina* occurs mainly in the 20-50 m zone under moderately reducing conditions (Sellier de Civrieux & Ruiz 1971). *Tolypammina* spp., although present in both facies, were much more common in the limestone facies. Overall the forms found only in the limestones include those considered to belong to a mixed energy, perhaps high turbulence, environment (McClellan 1966, 1973). However many more data are required before facies dependence of many of the species and genera can be confidently accepted although it would seem that some of the species found can tolerate lower oxygen conditions than others. The rate of deposition of the Taravale formation was probably rapid leading to a high input of organic material and so

Limestone facies		Cosmopolitan
Psammosphaera cava	*Thurammina subsphaerica*	*Astrorhiza triquetra*
Rhabdammina proavita	*Thurammina tributa*	*Astrorhiza constans*
Saccorhiza surculus	*Thurammina focrstei*	*Astrorhiza sinus*
Stomasphaera cyclops	*Thurammina zaramama*	*Cystingarhiza corona*
Soros-jaera sp. cf. *S. confusa*	*Ordovicina eisenacki*	*Cystingarhiza tribrachia*
Saccammina biosculata	*Kerionammina prolata*	*Cystingarhiza furca*
Saccammina cumberlandiae	*Lituotuba helix*	*Cylindrammina stolonifera*
Stegnammina cylindrica	*Lituotuba torquata*	*Rhabdammina linearis*
Webbinelloidea crassus	*Tolypammina tanula*	*Hyperammina proboscis*
Hemisphaerammina sp.	*Ammovertella calyx*	*Pelosina grandaeva*
Metamorphina tholus	*Hormosina divitiae*	*Lagenammina sphaerica*
Patellammina prona	*Reophax troca*	*Lagenammina talenti*
Hyperammina reflua	*Thuramminoides sphaeroidalis*	*Lagenammina laxacolla*
Hyperammina sp.	Muddy facies	*Lagenammina ovata*
Thurammina echinata	*Cystingarhiza mawsonae*	*Tolypammina anguinea*
	Lagenammina stilla	

Table 2. Distribution of species within the various facies.

a greater bacterial decay rate and subsequent oxygen depletion which would limit the species present.

DISCUSSION

This study has shown that the lower Devonian deposits in southeastern Australia have a large and varied foraminiferal fauna. Foraminifera were never common in any of the samples — approximately 10 per kg of sediment treated, which can be compared with other Lower Palaeozoic reported findings of about 25/kg (Gutschick 1988), about 100/kg (Browne & Schott 1963) and about 85/kg (Ireland 1966). Nevertheless it was apparent that in samples which contained little or no fine silt or sandy fraction (the sparry bioclastics) the foraminiferans were extremely rare whereas in the more sandy/clayey samples the foraminiferal fauna was markedly richer; this relative abundance of the agglutinated foraminifers shows the importance of lithology in the study of Palaeozoic foraminiferal faunas — a point also made by Conkin (1961) and Conkin & Conkin (1964b). Also it was apparent (but not investigated quantitatively) that there was an almost inverse relation between the abundances of foraminifera and conodonts; this relationship between foraminifera and conodonts has been previously remarked upon (Cushman & Stainbrook 1943). The numbers, and indeed the presence, of a species can depend upon the acid treatment the rocks received (Gutschick 1986); this point has not been addressed in this study as all samples had been acetic acid treated when received.

The numbers of genera and species are similar to those described for other parts of the world, although the faunas show significant differences e.g. the presence in Victorian faunas of *Cystingarhiza* and *Astrorhiza* but the lack of *Ammodiscus*. Whether this is an age or facies difference is not yet apparent and must await further work on the Australian faunas.

ACKNOWLEDGEMENTS

REFERENCES

ADEGOKE, D. S., DESSAUVAGIE, T. F. J. & YOLUYE, V. L. A., 1969. *Hemisphaerammina*-like egg capsules of Neritina (Gastropoda) from Nigeria. *Micropaleontology* 15: 102–106.

ATKINSON, K., 1969. The association of living foraminifera with algae from the littoral zone, south Cardigan Bay. *Journal of Natural History* 3: 517–542, text-figs 1–6.

BARNARD, T. A., 1958. Some Mesozoic adherent foraminifera. *Palaeontology* 1(2): 116–124.

BELL, K. N. & BURN, R. F., 1979. On the identity of *Webbinella bassensis* Parr. *The Victorian Naturalist* 96: 198–199.

BERMUDEZ, P. J. & DE RIVERO, F. C., 1963. Estudio Sistematico de los Foraminiferos Quitinosos, Microgranulares y Arenaceos. Universidad Central de Venezuela, Caracas. 398 pp.

BRADY, H. B., 1879. Notes on some of the Reticularian Rhizopoda of the Challenger Expedition. 1. On new or little known arenaceous types. *Quarterly Journal of Microscopical Science* 19: 20–63, 3 pls.

BRADY, H. B., 1884. Report on the foraminifera dredged by H.M.S. "Challenger" during the years 1873–1876. *Report, voyage of the Challenger, Zoology* 9, pp. 1–814, pls 1–115.

BRONNIMANN, P. & WHITTAKER, J. E., 1980. A revision of *Reophax* and its type species, with remarks on several other Recent hormosinid species (Protozoa: Foraminiferida) in the collections of the British Museum (Natural History). *British Museum, Natural History, Bulletin (Zoology)* 39(5): 259–272.

BROWNE, R. G. & SCHOTT, Y. J., 1963. Arenaceous foraminifera from the Osgood Formation, at Osgood, Indiana. *Bulletins of American Paleontology* 46: 191–242.

BUCHANAN, J. A., 1960. On Jullienella and Schizammina, two genera of arenaceous foraminifera from the tropical Atlantic. *Journal of the Linnean Society of London* 44: 270–277.

CHAPMAN, F. A., 1933. Some Palaeozoic fossils from Victoria. *Proceedings of the Royal Society of Victoria* 45: 242–248.

CONKIN, J. E., 1961. Mississippian smaller foraminifera of Kentucky, southern Indiana, northern Tennessee and south-central Ohio. *Bulletins of American Paleontology* 43: 131–368.

CONKIN, J. E. & CONKIN, B. M., 1964a. Mississippian foraminifera of the United States. Part 1 — The Northview Formation of Missouri. *Micropaleontology* 10: 19–47, pls 1, 2.

CONKIN, J. E. & CONKIN, B. M., 1964b. Devonian foraminifera: Pt 1, The Louisiana limestone of Missouri and Illinois. *Bulletins of American Paleontology* 47: 53–105.

CONKIN, J. E. & CONKIN, B. M., 1968. A revision of some Upper Devonian foraminifera from Western Australia. *Palaeontology* 11: 601–609.

CONKIN, J. E. & CONKIN, B. M., 1982. North American Paleozoic agglutinate foraminifera. In *Foraminifera, Notes for a short course*, M. A. Buzas & B. K. Sen Gupta, eds, University of Tennessee, Dept Geological Science, Studies in Geology 6: 177–191.

CONKIN, J. E., CONKIN, B. M. & CANIS, W. F., 1968. Mississippian foraminifera of the United States. Pt. 3: The limestones of the Chouteau Group in Missouri and Illinois. *Micropaleontology* 14: 133–178.

CONKIN, J. E., CONKIN, B. M. & McDONALD, D., 1963. Mississippian smaller foraminifera from the southern peninsula of Michigan. *Micropaleontology* 9: 215–227, pl. 1.

CONKIN, J. E., CONKIN, B. M. & PIKE, J. W., 1965. Mississippian foraminifera, Pt. 2: The Hannibal Formation of Missouri and western Illinois. *Micropaleontology* 11: 335–359.

CONKIN, J. E., CONKIN, B. M., WALTON, M. M. & NEFF, E. D., 1981. Devonian and early Mississippian smaller foraminiferans of southern Indiana and northwest Kentucky. Field Trip No. 2, Geological Society of America, Annual Meeting, Cincinnata, Ohio. 25 pp.

CUSHMAN, J. A., 1905. Developmental stages in the Lagenidae. *The American Naturalist* 39: 537–553.

CUSHMAN, J. A. & STAINBROOK, M. A., 1943. Some foraminifera from the Devonian of Iowa. *Cushman Laboratory for Foraminiferal Research, Contributions*, 19: 73–79.

DUNN, P. H., 1942. Silurian foraminifera of the Mississippi Basin. *Journal of Paleontology* 16: 317–342.

EARLAND, A., 1933. Foraminifera. Part 2, South Georgia. *Discovery Reports, Vol. 7*: 27–138.

FLETCHER, K., 1963. The Snowy River Volcanics west of Buchan, Victoria. *Proceedings of the Royal Society of Victoria* 76: 169–179, 1 pl.

GASKIN, A. J., 1933. The geology of Bindi, Victoria. *Proceedings of the Royal Society of Victoria* 55: 81–105.

GEROCH, S., 1955. Saccamminoides, nowa otwornica z Eocenu Kapat Fliszowych. *Polskiego Towarzystwa Geologicznego, Rocznik* 23: 53–63.

GUTSCHICK, R. C., 1986. Middle Ordovician agglutinated foraminifera including *Reophax* from the Mifflin Formation Platteville Group of Illinois. *Journal of Paleontology* 60: 233–248.

GUTSCHICK, R. C. & TRECKMAN, J. F., 1959. Arenaceous foraminifera from the Rockford limestone of northern Indiana. *Journal of Paleontology* 33: 229–250.

HAYWARD, B. W. & GORDON, D. P., 1984. A new species of the agglutinated foraminifer *Jullienella* (Schizamminidae) from New Zealand. *Journal of Foraminiferal Research* 14: 111–114.

HENBEST, L. G., 1963. Biology, mineralogy and diagenesis of some typical Late Paleozoic sedentary Foraminifera and Algal-foraminiferal colonies. *Cushman Foundation for Foraminiferal Research. Special Publication 6.*

HILL, D., 1950. Middle Devonian corals from the Buchan district, Victoria. *Proceedings of the Royal Society of Victoria* 66: 137–164.

HOFKER, J., 1972. *Primitive Agglutinated Foraminifera.* E. J. Brill, Leiden. 95 pp.

IRELAND, H. A., 1956. Upper Pennsylvanian arenaceous foraminifera, Kansas. *Journal of Paleontology* 30: 831–864.

IRELAND, H. A., 1966. Silurian arenaceous foraminifera from subsurface strata of N-E Kansas. *Micropaleontology* 12: 215–234.

KAZMIERCZAK, J., 1973. *Tolypammina vagans* (Foraminiferida) as inhabitant of the Oxfordian Siliceous Sponges. *Acta Paleontologica Polonica* 18: 95–115.

KROMMELBEIN, K., 1954. Devonische ostracoden aus der gegend von Buchan und von der Kuste der Waratah Bay, Victoria, Australien. *Senckenbergiana Lethaea* 35: 193–229.

LOEBLICH, A. R. & TAPPAN, H., 1988. Foraminiferal Genera and their Classification. Van Nostrand Reinhold Co., New York. 2 vols, 2047 pp.

LOEBLICH, A. R. & TAPPAN, H., 1994. Foraminifera of the Sahul Shelf and Timor Sea. *Cushman Foundation for Foraminiferal Research, Special Publication* 31, 661 pp.

McCLELLAN, W. A., 1966. Arenaceous Foraminifera from the Waldron Shale (Niagran) of S-E Indiana. *Bulletins of American Paleontology* 50: 444–518.

McCLELLAN, W. A., 1973. Siluro–Devonian Microfaunal Biostratigraphy in Nevada. *Bulletins of American Paleontology* 62: 233–375.

MALEC, J., 1992. Arenaceous foraminifera from Lower–Middle Devonian boundary beds of western part of the Gory Swietokrzyskie Mtns. *Annales Societatis Geologrum Poloniae* 62: 269–287.

MAWSON, R., 1987a. Early Devonian conodont faunas from Buchan and Bindi, Victoria, Australia. *Palaeontology* 30: 247–293.

MAWSON, R., 1987b. Documentation of conodont assemblages across the Early Devonian–Middle Devonian boundary, Broken River Formation, North Queensland, Australia. *Courier Forschungsinstitut Senckenberg* 92: 251–273.

MAWSON, R., JELL, J. S. & TALENT, J. A., 1985. Stage boundaries within the Devonian: Implications for application to Australian sequences. *Courier Forschungsinstitut Senckenberg* 75: 1–16.

MAWSON, R., TALENT, J. A., BROCK, G. A. & ENGELBRETSEN, M. J., 1993. Conodant data in relation to sequences about the Pragian–Emsian boundary (Early Devonian) in South-eastern Australia. *Proceedings of the Royal Society of Victoria* 104: 23–56.

MOREMAN, W. L., 1930. Arenaceous foraminifera from

the Ordovician and Silurian of Oklahoma. *Journal of Paleontology* 4: 42–59.

MOREMAN, W. L., 1933. Arenaceous foraminifera from the lower Paleozoic rocks of Oklahoma. *Journal of Palaeontology* 7: 393–397.

NORVANG, A., 1961. Schizamminidae, A new family of Foraminifera. *Atlantide Report* 6: 169–201, 4 pls.

PEDDER, A. E. H., 1967a. *Lyrielasma* and a new related genus of Devonian tetracorals. *Proceedings of the Royal Society of Victoria* 80: 1–30.

PEDDER, A. E. H., 1967b. Lower Devonian Streptelasmatid, Linstroemiid and possible Amplexocariniid corals from Victoria. *Proceedings of the Royal Society of Victoria* 80: 107–130.

PHILIP, G. M., 1966. Lower Devonian conodonts from the Buchan Group, eastern Victoria. *Micropaleontology* 12: 441–460.

PLUMMER, H. J., 1945. Smaller foraminifera in the Marble Falls, Smithwick and lower Strawn strata around the Llano uplift in Texas. *University of Texas, Publication* 4401: 209–271.

RIPPER, E. A., 1937. On the Stromatoporoids of the Buchan District. *Proceedings of the Royal Society of Victoria* 50: 12–38.

SELLIER DE CIVRIEUX, J. M. & RUIZ, J. B., 1971. La influencia de los parametros fisico-quimicos del fondo en las facies de foraminiferos bentonicos. *Boletin, Instituto Oceanografico Universidad de Oriente* 10: 15–34.

SHCHEDRINA, Z. G., 1969. O nekotorykh iz memeniyakh v sisteme semeystv Astrorhizidae i Reophacidae (Foraminifera). [On some changes in the systematics of the families Astrorhizidae and Reophacidae (Foraninifera)]. *Voprosy Mikropaleontologii* 11: 157–170.

SIMPSON, A. J., BELL, K. N., MAWSON, R. & TALENT, J. A., 1993. Late Silurian (Ludlow) conodonts and foraminifers from Cowombat, SE Australia. *Memoir, Association of Australasian Palaeontologists* 15: 141–159.

STEWART, G. A. & LAMPE, L., 1947. Foraminifera from the Middle Devonian bone beds of Ohio. *Journal of Paleontology* 21: 529–536.

TALENT, J. A., 1956. Devonian brachiopods and pelecypods from the Buchan Caves Limestone, Victoria. *Proceedings of the Royal Society of Victoria* 68: 1–56.

TALENT, J. A., 1965. The stratigraphic and diastrophic evolution of central and eastern Victoria in Middle Palaeozoic times. *Proceedings of the Royal Society of Victoria* 79: 179–195.

TALENT, J. A., 1967. Eastern Victoria. *Australian–New Zealand Association for the Advancement of Science, Excursion Handbook*, Section C: 69–85.

TALENT, J. A., 1969. The geology of East Gippsland. *Proceedings of the Royal Society of Victoria* 82: 37–60.

TALENT, J. A., 1989. Transgression-Regression Pattern for the Silurian and Devonian of Australia. In *Pathways in Geology: essays in honour of Edwin Sherbon Hills*, R. W. LeMaitre, ed., Blackwells, Melbourne, 201–219.

TEICHERT, C., 1948. Middle Devonian goniatites from the Buchan district, Victoria. *Journal of Paleontology* 22: 60–67.

TEICHERT, C. & TALENT, J. A., 1958. Geology of the Buchan area, East Gippsland. *Geological Survey of Victoria, Memoir* 21, 56 pp.

VANDENBERG, A. H. M., 1988. Silurian–Middle Devonian. In *Geology of Victoria*, J. G. Douglas & J. A. Ferguson, eds, Geological Society of Australia, Melbourne, 103–146.

WEBBY, B. D., STEARN, C. W. & ZHEN, Y. Y., 1993. Lower Devonian (Pragian–Emsian) stromatoporoids from Victoria. *Proceedings of the Royal Society of Victoria* 105: 113–185.

WINCHESTER-SEETO, T. & BELL, K. N., 1994. Microforaminiferal linings from the Early Devonian of Eastern Australia, and their generic placement. *Journal of Paleontology* 68: 200–207.

WHYMPER, E., 1892. Travels amongst the Great Andes of the Equator. C. Shribner's Sons, New York. 456 pp.

THE HERPETOFAUNA OF THE CHINAMAN WELL AREA
OF THE BIG DESERT, VICTORIA

A. J. Coventry

Herpetology Department, Museum of Victoria, 71 Victoria Crescent, Abbotsford, Victoria 3067

COVENTRY, A. J., 1996:12:31. The herpetofauna of the Chinaman Well area of the Big Desert, Victoria. *Proceedings of the Royal Society of Victoria* 108 (2): 107–119. ISSN 0035-9211.

A survey of the herpetofauna of the Chinaman Well area in the Victorian Mallee provided new data on the reproductive biology, ecological preferences and diets of many species. The area was sampled both pre and post extensive wild fires. Based on these data species such as *Ctenophorus pictus* and *Ctenotus brooksii iridis* benefit from fire, while clapid and typhlopid snakes are adversely effected. Distribution of several species across the study area indicate that the Victorian Mallee is a transitional zone between the southeastern Bassian and Eyrean zoogeographic regions.

BETWEEN August 1979 and December 1980, a survey of the herpetofauna of the Chinaman Well (35°52'42"S,141°39'52"E) area of the Big Desert in north western Victoria was undertaken. The flora of this area is comprised of areas of semi arid heath, interspersed with areas of mallee eucalypts with porcupine grass, *Triodia irritans*, set in fairly high scattered sand dune country. Because of the relative inaccessibility of the area, its fauna is poorly known. Rawlinson (1966) and Littlejohn (1966) have provided the only comprehensive lists of reptiles and amphibians respectively, recorded from the Victorian Mallee. Mather (1979) reported on the herpetofauna from within the then confines of the Wyperfeld National Park, while Baverstock (1979) listed these fauna from Billiatt Conservation Park, in the South Australian Murray mallee, and Menkorst (1982) listed and reported on the fauna from the White Springs area of the Big Desert. One of the aims of this work was to determine the species occurring in the Chinaman Well area and to study the ecology of this fauna. Since Rawlinson's and Littlejohn's 1966 lists, our understanding of the herpetofauna of this region has been greatly enhanced, with new species being added, and other species being separated into more than 1 taxon. Herpetological nomenclature used follows Cogger (1992), apart from *Phyllodactylus marmoratus*.

As a result of major wild fires in January 1981, sites 6 and 7 were totally devastated, site 4, immediately inside the perimeter of the fire boundary, suffered a 'cool' burn, and site 5 while not burnt, was adjacent to a totally devastated area, and separated from the perimeter of the fire by only about 10 m. These sites, together with sites 3 and 8 as controls, were re-established in September of that year in an attempt to assess the effects of the fires on the herpetofauna. This assessment was possibly affected by drought, combined with severe frosts in 1982.

MATERIALS AND METHODS

Pre fire 13 sites were sampled (Table 1), sites being selected because of the different composition of the flora, soils and topography, to ensure as wide

Site No.	Location
1	2 km N.E. of Chinaman Well, 35°52'46"S,141°39'51"E
2	0.6 N.N.E. of Chinaman Well, 35°52'42"S,141°39'49"E
3	1.3 km N. of Chinaman Well, 35°52'44"S,141°39'54"E
4	2 km N.N.W. of Chinaman Well, 35°51'56"S,141°39'37"E
5	2.75 km N.N.W. of Chinaman Well, 35°51'40"S,141°39'17"E
6	3.3 km N.N.W. of Chinaman Well, 35°51'27"S,141°38'57"E
7	5.1 km N.N.W. of Chinaman Well, 35°50'46"S,141°38'05"E
8	2 km N. of Chinaman Well, 35°52'22"S,141°40'31"E
9	2.8 km N.E. of Chinaman Well, 35°52'14"S,141°41'02"E
10	3 km N.E. of Chinaman Well, 35°52'09"S,141°41'11"E
11	4.7 km E.N.E. of Chinaman Well, 35°51'42"S,141°42'05"E
12	6.2 km E.N.E. of Chinaman Well, 35°51'52"S,141°43'06"E
13	6.6 km E.N.E. of Chinaman Well, 35°51'40"S,141°43'29"E

Table 1. Location of sites.

a range of habitats as possible (Table 2). Each site comprised 2 drift fences made from nylon fly wire mesh, 30 m long and 13 cm high. The fences ran approximately north–south and east–west, and had 10 pit-fall traps consisting of round metal containers that were 23 cm in diameter and 28 cm deep. Traps were closed between trips. A total of 14 trips were made, covering all seasons and climatic conditions, and during these trips, traps were checked and cleared each morning and evening. Co-ordinates of sites have been recorded using a Pyxis Global Positioning System Receiver IPS-360. During sampling daily maximum and minimum temperatures were recorded using a Zeal thermometer. Rainfall was also recorded, using a Marquis '600' rain-gauge measuring in mm.

Vegetation Site	Soil	Aspect	Topography	Overstorey	Understorey
1	Red clay		Large plain	*Eucalyptus calycogona* and *Eucalyptus dumosa*	*Dodonaea bursariifolia*, *Melaleuca uncinata* and *Melaleuca lanceolata*
2	Red clay and friable sands	Western slope	Low sand dune	*Eucalyptus behriana*, *E. dumosa*, *Acacia pycnantha* and *Myocarpon platycarpon*	*Acacia* spp., *Melaleuca* spp. and *Cassia* spp.
3	White sand		Interdune plain	*Eucalyptus foecunda* and *Eucalyptus incrassata*	*Callitris verrucosa*, *Leptospermum laevigatum*, *Hakea muellerana*, *Grevillea pterosperma*, *Casuarina muellerana* and *Triodia irritans*
4	White sand		Interdune plain	*E. incrassata* and *E. foecunda*	*Casuarina pusilla*, *C. verrucosa*, *L. laevigatum* and *T. irritans*
5	White sand	Top of dune	Low dune	*E. incrassata* and *E. foecunda*	*M. uncinata*, *Baeckea behrii*, *Phebalium bullatum* and *T. irritans*
6	White sand	Top of dune	Large dune	*E. incrassata*	*M. uncinata*, *B. behrii*, *P. bullatum*, *Hibbertia stricta* and *Lasiopetalum bauerii*
7	White sand	Top of dune	Large dune	*E. incrassata*	*M. uncinata*, *B. bauerii*, *P. bullatum*, *Laiopetalum behrii*, *H. muellerana*, *Acacia calamifolia*, *Baeckia crassifolia* and *Hibbertia* spp.
8	White sand		Interdune plain	*E. incrassata* and *E. foecunda*	*C. pusilla*, *L. laevigatum*, *H. muellerana*, *Grevillea pterosperma*, *Acacia spinescens*, *Lepidosperma carphoides* and *T. irritans*
9	White sand on limestone		Interdune plain	*E. foecunda*	*C. pusilla*, *T. irritans*, *B. crassifolia* and *Callitrix tetragona*
10	White sand	South eastern slope	Long low dune	*E. incrassata* and *E. foecunda*	*C. pusilla*, *H. muellerana*, *T. irritans*, *C. verrucosa*, *C. tetragona* and *H. stricta*
11	White sand	South western slope	Gently rising dune	*C. pusilla*, *L. laevigatum* and *T. irritans*	*H. muellerana*, *G. pterosperma*, *Lepidospermum myrsinoides*, *C. tetragona*, *B. crassifolia*, *Aotis ericoides* and *Leucopoga rufus*
12	White sand	North eastern slope	Large dune	*E. incrassata* and *E. foecunda*	*C. muellerana*, *L. laevigatum*, *Banksia ornata*, *C. verrucosa*, *H. muellerana* and *A. ericoides*
13	White sand	Southern slope	Large dune	*E. incrassata*	*B. ornata*, *Casuarina* spp., *Leptospermum* spp., *Calythrix* spp., *B. crassifolia*, *Phyllota pleurandroides* and *Styphelia exarrhena*

Table 2.   Characteristics of sites.

RESULTS AND DISCUSSION

Pre fire 29 reptile and 2 amphibian species were recorded from the sites, representing the families Gekkonidae, Pygopodidae, Agamidae, Varanidae, Scincidae, Typhlopidae, Elapidae, and Myobatrachidae. Series of each species, where possible, were retained as specimens, and registered into the collections of the Museum of Victoria.

A total of 990 specimens were recorded from the study sites representing 11 648 pitfall day/nights, or 896 trap day/nights per site, plus some hand collecting of species, such as the larger pygopodids, which were not as prone as other species to being caught in, or were large enough to escape from the traps. The number of each species recorded from each site, and the months in which they were recorded are listed in Tables 3 and 4 respectively.

Post fire trapping was carried out on 13 occasions, involving 896 trap/day nights per site. These results are presented in tabular form (Tables 6–9).

NOTES ON SPECIES COLLECTED PRE FIRE

Order SQUAMATA

Family GEKKONIDAE Gray, 1825

Diplodactylus vittatus Gray, 1832

This species was trapped between the middle of August and the end of March, and came from varied habitats. Females were obtained between October and February. In October–November, both females had 2 oviducal eggs, the November

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	Totals
Diplodactylus vittatus	2	0	2	4	2	2	4	2	2	0	2	0	0	22
Lucasium damaeum	0	0	1	0	0	2	4	0	0	1	0	0	0	8
Phyllodactylus marmoratus	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Aprasia inaurita	2	0	2	0	0	4	5	0	0	0	1	1	0	15
Delma australis	2	4	1	4	5	1	0	0	0	1	3	5	0	26
Delma butleri	0	1	0	0	0	0	0	0	1	0	0	0	0	2
Lialis burtonis	0	1	1	2	0	1	0	0	0	0	0	0	0	5
Pygopus lepidopodus	0	0	1	0	2	0	1	1	0	1	1	0	0	7
Amphibolurus norrisi	8	1	1	4	9	4	1	1	5	2	1	4	1	42
Ctenophorus fordi	0	0	25	14	21	1	3	24	28	44	36	31	18	245
Ctenophorus pictus	1	3	5	9	5	11	8	3	3	10	7	11	3	79
Pogona vitticeps	1	0	0	3	0	1	1	2	0	1	3	0	1	13
Tympanocryptis l. lineata	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Varanus gouldii	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Varanus rosenbergi	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Ctenotus brooksi iridis	1	1	2	8	1	4	4	3	0	7	4	1	3	39
Ctenotus robustus	0	4	7	4	7	1	0	8	15	7	8	11	6	78
Ctenotus uber orientalis	10	6	1	4	4	5	5	7	1	2	2	7	1	55
Lerista bougainvillii	4	1	0	5	5	10	9	1	3	2	6	3	1	50
Menetia greyii	0	0	2	2	3	1	2	3	3	2	0	0	1	19
Morethia obscura	3	0	5	0	5	0	0	10	0	10	7	3	6	49
Tiliqua occipitalis	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Ramphotyphlops australis	0	0	1	0	1	0	0	0	0	1	0	0	0	3
Ramphotyphlops bituberculatus	1	13	1	0	0	2	0	2	3	1	0	0	0	23
Drysdalia mastersii	3	1	1	2	5	3	3	1	0	1	1	1	0	22
Echiopsis curta	0	1	0	0	0	1	0	6	1	0	0	0	0	9
Pseudonaja textilis	0	0	1	0	0	0	0	0	1	0	0	0	0	2
Suta nigriceps	0	0	6	2	0	1	2	0	3	1	0	0	1	16
Suta spectabilis	0	0	0	0	1	1	0	1	0	0	0	1	1	5
Limnodynastes d. dumerilii	7	8	1	1	1	1	1	2	1	0	2	2	0	27
Neobatrachus pictus	3	5	2	1	1	0	2	1	3	0	0	0	0	18
Totals	48	51	70	69	79	57	55	78	73	94	85	81	44	884

Table 3. Number of specimens of each species from each site.

specimen also had convoluted oviducts. Two females were collected in December, a juvenile without enlarged ovaries, suggesting that maturity is not attained in the first year. The other, an adult, contained 2 shelled eggs. The 3 specimens collected during January and February had no oviducal eggs present, the ovaries were only slightly enlarged, the oviducts were convoluted. Males were obtained each month between August and February. From August to December the testes were enlarged, the left testis length ranging from 6.6 to 7.8% of SVL. In January and February, the 2 males obtained had regressed testes of 3.1 and 4.6% SVL respectively, showing that males are in breeding condition from early spring until mid summer. Minimum temperatures recorded on successful trapping nights ranged from 6.5 to 23°C.

Rain fell during the night of 26/27 September when the minimum temperature was 13°C, and 2 mm fell during the night of 22/23 October when the minimum temperature was 23°C. One specimen was trapped on each of these 2 nights. For details of diet, refer to Table 5.

Lucasium damaeum (Lucas & Frost, 1896)

This species was trapped between the beginning of November and the end of February. All came from sites with deep sand, and all but 1 were recorded from dunes. Indications were that breeding took place in late spring. One female obtained on November had enlarged ovaries, 1 in December had 2 large oviducal eggs, while the 1 collected in February had slightly enlarged ovaries

Species	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Totals
Diplodactylus vittatus	2	4	1	0	0	0	0	1	2	4	6	2	22
Lucasium damaeum	0	3	0	0	0	0	0	0	0	0	4	1	8
Phyllodactylus marmoratus	0	0	0	0	0	0	0	0	0	0	1	0	1
Aprasia inaurita	1	0	0	0	0	0	0	0	0	11	1	2	15
Delma australis	0	9	2	0	0	0	0	3	1	3	4	4	26
Delma butleri	0	0	0	0	0	0	0	0	0	0	1	1	2
Lialis burtonis	0	1	0	0	0	0	0	1	0	0	2	1	5
Pygopus lepidopodus	1	2	0	0	0	0	0	1	0	0	1	2	7
Amphibolurus norrisi	3	4	10	0	0	0	0	0	3	3	12	7	42
Ctenophorus fordi	20	47	31	0	0	0	0	0	21	42	23	61	245
Ctenophorus pictus	3	26	21	1	0	0	0	1	6	1	13	7	79
Pogona vitticeps	0	5	3	0	0	0	0	0	0	3	1	1	13
Tympanoctryptis l. lineata	0	0	0	0	0	0	0	0	0	0	0	1	1
Varanus gouldii	0	1	0	0	0	0	0	0	0	0	0	0	1
Varanus rosenbergi	0	0	1	0	0	0	0	0	0	0	0	0	1
Ctenotus brooksi iridis	3	15	0	0	0	0	0	0	1	1	15	4	39
Ctenotus robustus	4	28	23	0	0	0	0	0	1	4	3	15	78
Ctenotus uber orientalis	3	25	6	0	0	0	0	0	4	7	4	6	55
Lerista bougainvillii	3	6	1	0	0	0	0	0	0	10	29	1	50
Menetia greyii	0	0	1	1	0	0	0	1	2	2	9	3	19
Morethia obscura	5	10	6	0	0	0	0	3	3	7	8	7	49
Tiliqua occipitalis	0	1	0	0	0	0	0	0	0	0	0	0	1
Ramphotyphlops australis	0	0	0	0	0	0	0	0	0	3	0	0	3
Ramphotyphlops bituberculatus	4	0	0	0	0	0	0	0	0	8	7	4	23
Drysdalia mastersii	1	1	7	1	1	0	0	0	5	2	0	4	22
Echiopsis curta	2	1	0	1	0	1	0	0	0	3	0	1	9
Pseudonaja textilis	0	0	0	0	0	0	0	0	0	2	0	0	2
Suta nigriceps	1	3	2	0	0	0	0	0	2	5	1	2	16
Suta spectabilis	0	0	1	0	0	0	0	0	1	1	1	1	5
Limnodynastes d. dumerilii	0	0	0	0	0	0	0	0	24	3	0	0	27
Neobatrachus pictus	0	0	0	0	0	0	0	4	14	0	0	0	18
Totals	56	192	116	4	1	1	0	15	90	125	146	136	884

Table 4. Number of each species recorded each month.

Prey item	Species						
	D. vittatus (12)	D. australis (19)	C. fordi (107)	C. pictus (67)	P. vitticeps (22)	C. uber (34)	M. obscura (62)
Arachnida							
Araneae	25	52.6	8.4	17.9	13.0	31.2	53.2
Scorpionida	16.7	0	0	0	0	0	0
Blattodea	75	42.1	0.9	3	9	21.9	12.9
Chilodopa	0	0	0	0	9	6.1	0
Coleoptera	0	10.5	49.5	23.9	81	21.9	19.7
Diplopoda	0	0	0	0	4	0	0
Diptera	0	0	8.4	3	0	0	11.7
Hemiptera	8.3	0	0	25.4	31	9.4	53.2
Hymenoptera							
Apoidea	0	0	23.8	7.5	0	6.3	6.5
Formicidae	33.3	0	97.2	98.5	86	40.6	11.7
Mutilidae	0	0	0	0	0	6.3	0
Gordiidae	0	0	0	0	0	0	1.6
Isoptera	0	0	0	0	0	21.9	1.6
Leafhoppers	0	0	0	1.5	0	0	0
Lepidoptera	0	10.5	7.5	9	18	18.8	12.9
Mollusca	0	0	0	0	0	3.1	1.6
Neuroptera	0	0	0.9	0	0	0	1.6
Odonata	0	0	0.9	0	0	0	0
Orthoptera	16.7	10.5	0	6	22	12.5	0
Plant material	0	0	0	0	4	15.6	0
Psyllidae	0	0	0	0	0	0	1.6
Thysanura	0	0	0	0	0	3.1	0
Vertebrata	0	0	0	0	9	0	0

Table 5. Stomach contents of *Diplodactylus vittatus, Delma australis, Ctenophorus fordi, Ctenophorus pictus, Pogona vitticeps, Ctenotus uber orientalis* and *Morethia obscura*. Numbers in the table show the percentage of specimens examined in which the prey item was present, the numbers in parentheses after the species indicate the number of stomachs examined.

and convoluted oviducts. In males, the 3 recorded in November had enlarged testes, the length of the left testis ranging between 10.5 and 14.1% of SVL, while the 2 collected in February had regressed testes, ranging from 5.2 and 5.3% of SVL. Minimum overnight temperatures recorded on nights when this species were trapped ranged from 4.0 to 23°C. No rainfall was recorded on successful trap nights. No specimens had food remains in the gut.

Phyllodactylus marmoratus (Gray, 1847)

This species was very uncommon within the study area, only 1 specimen was trapped, in November 1980 at site 2. Three specimens were collected by hand.

Species	Site number					
	3	4	5	6	7	8
Aprasia inaurita	1	0	0	0	0	0
Amphibolurus norrisi	0	1	0	0	0	0
Ctenophorus fordi	5	3	5	0	0	3
Ctenophorus pictus	1	0	1	0	0	0
Ctenotus brooksi iridis	0	1	2	1	0	4
Lerista bougainvillii	0	0	0	0	1	0
Menetia greyi	1	0	3	0	0	0
Morethia obscura	1	2	6	2	0	0
Limnodynastes d. dumerilii	0	0	0	2	2	1
Neobatrachus pictus	0	0	0	0	4	0

Table 6. Number of specimens of each species collected at each site during 1981 (180 trapping day/nights). One specimen of *Tiliqua occipitalis* was collected by hand from site 3.

Species	Site number					
	3	4	5	6	7	8
Diplodactylus vittatus	0	0	0	2	0	1
Lucasium damaeum	0	0	0	0	1	0
Aprasia inaurita	0	0	1	1	0	0
Delma australis	1	0	0	0	0	0
Delma butleri	0	0	2	0	0	0
Amphibolurus norrisi	0	0	2	1	0	0
Ctenophorus fordi	4	7	12	2	4	11
Ctenophorus pictus	3	5	0	8	14	6
Pogona vitticeps	0	0	0	1	0	0
Ctenotus brooksi iridis	3	4	0	4	2	6
Ctenotus robustus	2	1	2	2	0	1
Ctenotus uber orientalis	0	2	1	1	3	0
Lerista bougainvillii	0	0	0	1	3	0
Menetia greyii	0	1	0	0	0	0
Morethia obscura	3	5	1	0	1	3
Drysdalia mastersii	0	0	2	0	0	0
Echiopsis curta	0	0	0	0	0	1

Table 7. Number of specimens of each species collected at each site during 1982 (180 trapping day/nights).

Species	Site number					
	3	4	5	6	7	8
Diplodactylus vittatus	1	0	0	1	1	0
Lucasium damaeum	0	0	0	0	1	0
Aprasia inaurita	1	1	0	0	0	0
Amphibolurus norrisi	0	1	0	0	0	0
Ctenophorus fordi	6	4	2	1	1	9
Ctenophorus pictus	2	14	1	5	36	5
Pogona vitticeps	0	1	0	0	0	0
Ctenotus brooksi iridis	2	1	0	2	3	3
Ctenotus robustus	1	0	2	0	0	3
Ctenotus uber orientalis	0	0	1	0	1	0
Lerista bougainvillii	0	0	0	0	1	0
Menetia greyii	0	0	0	0	1	0
Morethia obscura	1	1	0	0	0	1
Ramphotyphlops australis	2	0	0	0	0	0
Ramphotyphlops bituberculatus	1	0	0	0	0	0
Echiopsis curta	0	1	0	0	0	0
Suta nigriceps	0	1	0	0	0	0
Neobatrachus pictus	0	1	0	0	0	0

Table 9. Number of specimens of each species collected at each site during 1984 (396 trapping day/nights).

Species	Site number					
	3	4	5	6	7	8
Diplodactylus vittatus	0	1	0	2	0	0
Lucasium damaeum	0	0	0	0	2	0
Delma australis	1	0	0	0	0	0
Delma butleri	0	0	0	0	0	1
Amphibolurus norrisi	0	0	1	1	2	0
Ctenophorus fordi	2	2	3	0	1	11
Ctenophorus pictus	2	7	2	2	7	0
Ctenotus brooksi iridis	0	2	0	1	0	6
Ctenotus robustus	2	1	2	0	0	0
Ctenotus uber orientalis	0	3	0	2	1	0
Lerista bougainvillii	0	2	0	2	2	0
Menetia greyii	0	0	1	0	0	0
Morethia obscura	0	1	0	0	0	0
Ramphotyphlops australis	0	0	0	1	0	0
Ramphotyphlops bituberculatus	0	0	0	0	0	1
Drysdalia mastersii	0	0	1	0	0	0
Echiopsis curta	0	0	1	0	0	0
Suta nigriceps	1	0	0	0	1	1
Limnodynastes d. dumerilii	1	0	1	0	0	0

Table 8. Number of specimens of each species collected at each site during 1983 (240 trapping day/nights).

Family PYGOPODIDAE, Gray, 1845

Aprasia inaurita Kluge, 1974

This species was only trapped between mid October and mid January. All were taken from traps in the evening, indicating they were diurnal, and all were trapped on days when the maximum temperature was at least 25°C. This finding contrasts with Cogger et al. (1983), who state that the species is nocturnal. Three of the specimens were female, the 2 obtained in October each having 2 oviducal eggs, while the 1 obtained in January had slightly enlarged ovaries, and convoluted oviducts. The males had testis length ranging from 5.8–7.9% of SVL in October, N=9, while in December they had regressed to 3.1–3.8% SVL, N=2. These data show an apparent peak of activity at the onset of warm weather, probably associated with males searching for breeding partners. Three specimens had food remains present, in each case consisting of small ant eggs. These specimens were collected from sites 6 and 7. Table 3 shows that 60% of the specimens collected came from these 2 sites. Both sites had numerous nests of ants of the genus *Aphaenogaster*.

Delma australis Kluge, 1974

Forty-nine specimens were examined from the area during the survey, 26 being taken in traps. The species was common, and readily obtained under *Triodia* or ground creepers. Based on testis length expressed as a percentage of SVL length, male breeding begins in late winter when the testis % of SVL ranged from 9.45 to 13.69,

M = 12.02, N = 5 during August; 10.29 to 12.81, M = 11.7, N = 5 in September, and 11.71 to 15.06, M = 14.11, N = 3 in October, and then declined in late spring and early summer when they ranged from 5.4 to 9.7, M = 8.16, N = 3 in November, from 4.4 to 7.69, M = 6.53, N = 5 in December and 4.8 to 7.33, M = 5.74, N = 4 in February. Females collected in August and September had several enlarged ovarian follicles present. In October and December respectively, 1 female was examined, and each had 1 egg present in each oviduct. Maturity appears to be attained at a SVL length of approximately 60 mm. The smallest reproductively active male was a September specimen with an SVL of 62.6 mm, with testis 11.54% of SVL. The largest immature female (SVL 59 mm) was taken in August and the smallest reproductively active female (SVL of 67 mm) a gravid specimen taken in December. Stomach contents were consistent with the invertebrates common in *Triodia* habitats (see Table 5).

Delma butleri Storr, 1987

Only 2 specimens were trapped (site 2 November 1980 and site 9 December 1980). An additional 10 specimens were collected by hand from sites 5, 3, and 2 from a few km SSE of Chinaman Well. Of the 2 specimens with food in their stomachs, 1 had remains of a lepidopteran, the other remains of a blattodid. Females had ovarian follicles present in August, and 1 specimen had 2 oviducal eggs in November. Patchell & Shine (1986) discuss aspects of the ecology of this species.

Lialis burtonis Gray, 1835

Both colour morphs of this species were obtained, 13 plain, comprising 6 males and 7 females, and 5 striped, 1 male and 4 females. All but 5 of these specimens were collected by hand near site 5. Despite the low sample size, there was some indication that females attain a greater SVL than males. Cogger et al. (1983) and Bustard (1970) reported that this species is lacertiphagous. Only 1 stomach examined contained food, a specimen of *Menetia greyii*.

Pygopus lepidopodus (Lacepede, 1804)

This species was widespread, and active from early spring through to late summer. No specimens examined had food in their stomachs.

Family VARANIDAE Hardwicke & Gray, 1827

Varanus rosenbergi Mertens, 1957

Only 1 specimen was trapped. A road kill in November 1980, 17 km WNW of Chinaman Well and a third specimen, a gravid female 0.6 km NW of Chinaman Well in December 1981 have also been obtained. This species appears to inhabit mallee heath in the interior of the Big Desert well isolated from agricultural areas.

Varanus gouldii (Gray, 1838)

Two specimens were recorded, a hatchling from site 13 and an adult male near site 11, both areas being relatively close to agricultural areas.

Family AGAMIDAE Gray, 1827

Amphibolurus norrisi Witten & Coventry, 1984

This species was collected at all sites. The 2 sites where it was most often recorded, 1 and 5, both had a comparatively high percentage of mallee eucalypts forming the upper canopy. It was often seen basking on low shrubs, or flattened *Triodia*. Reproductive and diet data for this species were listed by Witten & Coventry (1984).

Ctenophorus fordi (Storr, 1965)

This species has been studied and reported on by Cogger (1974, 1979). In January, February and March, hatchlings which had obtained an SVL in excess of 30 mm were still immature, and in those mature specimens which had survived, the testes had regressed. From September to December, almost all males in excess of 30 mm SVL were mature and ready for breeding. Those which were immature were possibly late hatchlings, which would survive to breed the following year. Females examined during October, November and early December each had 2 oviducal eggs present. Only 1 female was examined (October) which had survived after breeding the previous year. There was a bias of males towards females of 1 − 0.42. Those sites with little or no *Triodia* (1, 2, 6 and 7) produced only 4 specimens between them, demonstrating that it is a *Triodia* dependent species (Table 3). Diet analyses are presented in Table 5.

Ctenophorus pictus (Peters, 1866)

This species was widely distributed over the study area, being recorded from all sites. Sites, 6, 10 and

12, with traps on or down the sides of dunes accounted for 40% of the specimens trapped. Seventy per cent of specimens were recorded during the day, demonstrating that it is largely diurnal. Maximum temperatures when the lizard was collected ranged from 16°C to 45°C. Only 1 female was collected during August, this specimen had enlarged ovaries. Females had from 1-4, M = 2.6, N = 8 oviducal eggs present from October to December. By January, all females collected were hatchlings. Testes size appears to increase with the size of specimens, until a peak in late spring and early summer, with a decrease in January. The January male with a testis length of 4.4 mm had a SVL 58.4 mm, in comparison to a December specimen with testis length of 6.4 mm, and SVL of 58.1 mm, suggesting a reduction in reproductive activity. There was a bias of males towards females of 1 − 0.53. A minority of the population appear to survive to a second breeding season. Dietary analyses are presented in Table 5.

Pogona vitticeps (Ahl, 1926)

For comments on the relationships of this species see Witten & Coventry (1990). Table 5 summarises the diet. In males testes size reached a peak in late summer. Eggs were present in the oviducts of females until mid December. The maximum number of eggs recorded was 10, the minimum 7, M = 8; N = 7. Overall, the ratio of males : females was 1:2, with the ratio for February and March being 1:1, and for August to January, when the females were more active presumably to facilitate breeding, 1:4.5.

Tympanocryptis l. lineata Peters, 1863

Only 1 specimen of this species, a female, snout-vent length 45 mm, was recorded. It was trapped at site 5 during December 1979.

Family SCINCIDAE Gray, 1825

Ctenotus brooksi iridis Storr, 1981

This widely distributed species was found at all sites except 9. No particular habitat or soil type seemed preferred, although the hard soils of site 1 and the open habitat of site 2 produced only 1 specimen each. Most commonly recorded during November and February (Table 4). No analyses of stomach contents or gonads were carried out, as the specimens constitute the type series.

Ctenotus robustus Storr, 1970

The largest Ctenotus in the study area. It was widespread and common, although not recorded from sites 1 and 7. Most common at sites 9 and 12, in contrast to C. uber orientalis which was most prevalent on site 1, and least common at sites 3 and 13 (Tables 3, 4). C. robustus appears to emerge slightly later than C. uber orientalis, with only 7% of specimens being recorded during September and October, and 22.5% during November and December, as against 22.3% and 11.1% respectively. Correspondingly, C. robustus appears more active later in the year with 29.6% of specimens being recorded in March; only 13.3% for C. uber orientalis. Female reproductive data was confined to 6 specimens considered to be mature. These ranged from 85.1-105.3 mm SVL. The 3 December specimens each had 6 oviducal eggs, while the 2 January and 1 February specimens had convoluted oviducts. Fifteen mature males were examined, the testes were enlarged during late spring and early summer, but had regressed by early autumn. Breeding males had broad testes when compared with non breeding specimens. Specimens do not breed until their second year, a 1 year old female collected in December having an SVL of 56.7 mm and a 1 year old male, also collected in December having an SVL of 71.2 mm. The smallest hatchling collected had an SVL of 34.7 mm. Brown (1983) provided diet analyses for specimens from this survey.

Ctenotus uber orientalis Storr, 1971

This species although common and widespread, preferred the harder, more reddish soils, such as site 1 where most recordings occurred. The largest specimen recorded was a female taken in December, with an SVL of 71.4 mm. None of the adult females sampled (2 in September and 3 in December) had oviducal eggs present although all had convoluted oviducts. The smallest breeding female had an SVL of 57.2 mm. In males testes were enlarged by September and had started to regress by January. This suggests that this species breeds slightly earlier in the season than C. robustus. The smallest adult male had an SVL of 58.5 mm. The smallest hatchling collected had an SVL of 24.7 mm. For details of diet see Table 5.

Lerista bougainvillii (Gray, 1839)

This species was common and widespread, although showing an apparent preference for

sandy substrates. Sites such as 6 and 7 were most preferred. Qualls et al. (1995) discussed the evolution of viviparity within this species. Specimens from the study area were oviparous. Cogger et al. (1983) list this species as being an arthropod feeder.

Menetia greyii Gray, 1845

The smallest member of the skink family in the study area. The smallest specimen examined had an SVL of 19.8 mm, while the largest specimen had an SVL of 33.1 mm, with females being slightly larger size than males, ranging from 20.8 mm to 33.1 mm SVL, M = 27.6, N = 13, and males ranging from 19.8 mm to 29.9 mm SVL, M = 26.1, N = 17. The species was widespread, most specimens trapped being recorded during November. Although recorded from other areas where *Triodia* is absent, it is interesting to note that within the study area, it was not, or infrequently trapped where *Triodia* was absent or sparse. Mating appears to take place during late spring–early summer, females laying 2 eggs in mid summer. One September female had enlarged ovarian follicles present and convoluted oviducts, and 2 specimens collected in November each had 1 oviducal egg present in each oviduct, which were convoluted. In the males the testes are enlarged during September and October, when they are between 14 and 18.5% of SVL, M = 15.3%, N = 4 and start regressing during November and December, when they drop back to between 11.7 and 15.5% of SVL M = 12.9%, N = 10.

Morethia obscura Storr, 1972

A common and widespread species which is active throughout the year excepting winter. Females lay 2–3 eggs in early to mid summer. By the end of January, egg laying had ceased. By August the ovaries are beginning to become enlarged, and by October oviducal eggs are present. In males the testes attain their greatest size in August, and by December are starting to recede. For details of diet see Table 5.

Tiliqua occipitalis (Peters, 1863)

Only 1 specimen was trapped, a juvenile male, recorded in February from site 11.

Trachydosaurus rugosus Gray, 1825

Although observed and widespread in the area, this species was not taken in pitfall traps.

Family TYPHLOPIDAE Jan, 1863

Ramphotyphlops australis (Gray, 1845)

This species was only collected on the night of 22/23 October 1980, with individual specimens being trapped on sites 3, 5 and 10. This night was warm and humid, with a minimum temperature of 20°C. 2 mm of rain was also recorded. All specimens were males, ranging in SVL from 291 mm, to 261 mm. Testis length ranged from 3.5 to 4.8% of SVL length. All specimens lacked stomach contents.

Ramphotyphlops bituberculatus (Peters, 1863)

Most commonly recorded from site 2. All sites where this species was collected excepting site 1, had sandy substrates.

Family ELAPIDAE Boie, 1827

Drysdalia mastersii (Krefft, 1866)

The most common elapid trapped or observed during the survey, and one of the 2 diurnal species. It was widespread, being recorded from all sites. It was also active for a consistently greater period of the year than other species, being trapped as late as May, and observed as early as August. Stomach contents consisted of skinks, 4 specimens had remains of *Morethia obscura*, 2 of *Lerista bougainvillii*, 1 a juvenile *Ctenotus robustus*, and 2 unidentifiable skinks and ant remains. It is assumed that the ant remains were from the stomachs of prey items. In males the testes become enlarged in January, and remain enlarged until the beginning of winter, regressing by spring. Although the current sample size is small it would suggest that the species mate soon after the females give birth, and in the light of Shine's findings (1981), would suggest that the females store sperm over winter. Shine (1977a) records that in some other live bearing elapids mating takes place in autumn soon after parturition, and also in spring. For further information of the ecology of this species see Shine (1981).

Echiopsis curta (Schlegel, 1837)

A nocturnal species, most commonly trapped on site 8. Of the 3 the females, 1, collected in October with an SVL of 320 mm, had 7 oviducal embyros. The other females were both collected in January. One was immature with an SVL of 178 mm, the other an adult with an SVL of

331 mm. The largest specimen collected was a male, SVL 331 mm. Only 3 specimens had food items present, and these consisted of a *Ctenophorus fordi*, a *Morethia obscura* and a *Ninguai* sp. (Coventry & Dixon 1984).

Pseudonaja textilis (Dum. Bib. & Dum. 1854)

The largest and only oviparous elapid in the area was only trapped twice, once at site 3 and once at site 9, both times during October. The specimen from site 3 was a juvenile, the specimen from site 9 just over 1 m in length. When collected, this specimen was preying on a trapped *Amphibolurus norrisi*. Several other specimens were observed both in the study area, and on the surrounding farm lands.

Suta nigriceps (Gunther, 1863)

This nocturnal species was only located by pitfall trapping. On previous occasions the author has collected desert heath specimens from under iron, and also under a rock. Of the 16 specimens, 7 had food remains in the gut. All food remains were of lizards. All specimens were males, ranging in size from 153–369 mm SVL. In adults, testes size ranged from 1–4.4% of SVL length, with no noticeable trends towards being enlarged at any particular season (Jan. 3.7; Feb. 3.2; Mar. 2.3; Oct. 2.5, N = 2; Nov. 3.0; Dec. 1.0, N = 1. It is expected that this species would mate in autumn.

Suta spectabilis (Krefft, 1869)

This strictly nocturnal species was also only located by trapping. It is presumed to be widespread throughout the area, but less common than *Suta nigriceps*. The smallest specimen a female had an SVL of 141 mm. The other 4 specimens, males, ranged from SVL 233 mm to 261 mm. The September and October specimens had testes lengths 2.7 and 2.3% of SVL respectively while the March specimen had testes length of 4.1% of SVL, suggesting that breeding takes place in late summer and early autumn, with the young being born in spring or early summer. This would concur with the findings of Shine (1977b). Only 1 of the specimens had any food in the gut, the tail of a scincid lizard.

Order SALIENTIA

Family MYOBATRACHIDAE Schlegel,1850

Only 2 species of amphibians, *Limnodynastes*

dumerilii dumerilii Peters, 1863, and *Neobatrachus pictus* Peters, 1863, were recorded, although other species (e.g. *Limnodynastes tasmaniensis* Gunther, 1858; *Neobatrachus sudelli* (Lamb, 1911) and *Pseudophryne bibroni* Gunther, 1858) have been recorded from adjacent areas (Brook 1982). Both species are burrowers, and proved extremely common in suitable conditions. In the September sample, when over 20 mm of rain fell, a total of 39 specimens were recorded. In October 1979, a dry month, only *L. d. dumerilii* was recorded and in August 1980, when 6.7 mm of rain fell, only *N. pictus* were recorded. Eggs of this species were laid in temporary ponds, where wastage was extremely high. No analyses were made of gut contents or gonads.

DISCUSSION OF VICTORIAN SEMI-ARID HERPETOFAUNA

Abundance

Pre fire a total of 36 elapid and 26 typhlopid snakes were trapped while post fire only 9 elapid, 2 of which were recorded from the unburnt control sites, and 5 typhlopid specimens, were recorded. The first elapid was not recorded until February–March 1982, and only 3 were recorded prior to September 1983, the first typhlopid recorded in November–December 1983. This suggests that snakes have little protection from wild fires, and/or that those that do survive the fires are easy victims of predators. There was also a marked difference between the comparative numbers of the 2 species *Ctenophorus fordi* and *Ctenophorus pictus* pre and post fire. This is demonstrated in Table 10, where the percentage of *C. pictus* recorded was 31.8 pre and 54.6 post fire. If the results obtained from sites 3 and 8 post fire are ignored, i.e. the unburnt control sites, the percentage of *C. pictus* recorded was 46.6 pre fire and 67.5 post fire. In the figures for site 5 the percentages were 57.1 pre fire and 77.5 post fire. While these figures tend to demonstrate that sites 4, 6 and 7 were more attractive to *C. pictus* pre fire, they do demonstrate that *C. pictus* appears to prefer the more open areas provided in habitats with little or no *Triodia*. At site 7, the most open site pre fire, and the most heavily burnt, the percentage of *Ctenophorus* recorded which were *C. pictus* constituted 72.7 pre and 95.1 post fire. Also, Tables 6 and 7 demonstrate that in the immediate season post fire, numbers of both species were well maintained, but that *C. fordi* numbers then began to drop off, before recovering, presumably attributable to the

Species	Site number												Totals	
	3		4		5		6		7		8			
	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Diplodactylus vittatus	2	1	4	3	2	1	2	5	1	1	2	4	16	15
Lucasium damaeus	1	0	0	0	0	0	4	4	4	4	0	0	7	4
Aprasia inaurita	2	2	0	1	0	1	5	1	5	1	0	0	11	6
Delma australis	2	2	4	1	5	1	1	1	1	1	0	2	11	4
Delma butleri	3	0	0	0	1	1	0	0	1	0	0	0	7	1
Lialis burtonis	1	0	2	0	4	0	0	0	0	0	0	0	4	1
Pygopus lepidopodus	1	0	2	0	0	0	0	0	0	0	0	0	5	0
Amphibolurus norrisi	1	1	0	0	2	0	4	2	1	1	1	1	20	11
Ctenophorus fordi	25	20	14	17	21	26	1	4	3	3	24	34	88	104
Ctenophorus pictus	5	8	9	27	5	4	11	15	8	58	3	13	41	125
Pogona vitticeps	0	0	3	1	1	0	1	1	1	1	2	0	8	3
Tympanocryptis l. lineata	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Varanus rosenbergi	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Ctenotus brooksi iridis	2	6	8	8	8	4	4	8	4	22	3	1	22	49
Ctenotus robustus	7	7	4	3	7	6	1	2	0	0	8	4	27	22
Ctenotus uber orientalis	1	2	4	7	4	5	5	4	5	7	7	1	26	26
Lerista bougainvillii	0	0	5	2	5	0	10	4	9	7	1	0	30	13
Menetia greyii	2	0	2	1	3	2	1	0	2	1	3	2	13	7
Morethia obscura	5	5	0	9	5	9	0	4	0	4	10	4	20	35
Ramphotyphlops australis	1	2	0	0	1	0	0	1	0	0	0	2	2	3
Ramphotyphlops bituberculatus	1	0	2	0	0	0	2	0	3	0	2	1	5	2
Drysdalia mastersii	1	0	0	0	5	3	3	0	0	0	1	0	15	3
Echiopsis curta	0	0	0	0	0	0	1	0	0	0	6	0	7	0
Pseudonaja textilis	1	0	2	1	0	0	0	0	2	1	0	0	1	0
Suta nigriceps	6	1	0	0	0	0	2	0	0	0	0	1	11	4
Suta spectabilis	0	0	0	0	1	0	0	0	0	0	1	1	3	0
Limnodynastes d. dumerilii	0	1	1	0	1	1	2	2	1	2	12	1	7	7
Neobatrachus pictus	2	0	1	1	0	0	0	0	2	4	1	0	7	5

Table 10. Comparison of total catches at each site pre and post fire.

paucity of *Triodia*. On the other hand, *C. pictus* numbers showed rapid increase with the additional open areas available to them. Percentage wise, 44.9% of *C. fordi* recorded were pre fire, compared with only 24.6% of *C. pictus*. In the case of the 3 *Ctenotus* species, numbers of both *Ctenotus robustus* and *Ctenotus uber orientalis* remained fairly static, whereas *Ctenotus brooksi iridis* appear to prefer the more open areas post fire, with only 29.3% of the total catch being pre fire.

Zoogeography

Spencer (1896) divided Australia into 3 main zoogeographic regions, Torressian (monsoonal), Eyrean (arid and semi-arid) and Bassian (higher rainfall SE and SW of Australia). Other workers e.g. Littlejohn (1971) have basically agreed with Spencer's concept. Rawlinson (1971) divided Victoria into 2 main regions (Eyrean and Bassian), which he further subdivided. Thus his Eyrean region included 'true Eyrean' and 'Murray River corridor', and his Bassian 'warm temperate', 'cool temperate' and 'cold temperate'. Those areas under discussion fall into his 'true Eyrean' zone.

Some eyrean, species such as *C. pictus* occur widely and are very common as far south as the southern edge of the Little Desert, others such as *C. fordi* reach their southern limit in the south of the Big Desert. In the south, *A. inaurita* is replaced by *Aprasia striolata*, while *Lampropholis delicata* does not occur north of the Little Desert. South of Chinaman Well towards Netherby, *Pogona barbata*, a Bassian species, replaces the Eyrean *P. vitticeps*. True Eyrean species such as *Pseudonaja nuchalis*, *Rhynchoedura ornata* and *Heteronotia binoei* are found only in the northern areas, suggesting that the Victorian Mallee is a transitional zone between the southeastern Bassian and Eyrean zoogeographic regions.

While amphibians can be divided into zoo-geographic regions, rivers and lakes cause artificial overlaps. The Murray River corridor and the lake systems thus affect this Victorian Mallee fauna.

Diversity

Lizard species diversity within the Big Desert areas agree with the findings of Pianka (1986), who found that the Great Victorian Desert in Western Australia had both a high number of species and high species population densities. The numerous micro-environments in desert heath provide ample opportunity for species specialisation, and habitat partitioning by the lizard fauna. Skinks were the most diverse family, with the *Morethia boulengeri* complex represented within the mallee by 3 species, each with its own habitat niche. Snakes on the other hand were poorly represented, with 71% of the species being nocturnal, of these 80% were fossorial. The presence of only 2 species of diurnal elapids was possibly due to the presence of large potential predators. This theory is supported by the fact that only snakes, over 1 metre in length, were observed basking or moving.

REFERENCES

BAVERSTOCK, P., 1979. A Three Year Study of the Mammals and Reptiles of Billiatt Conservation Park in the Murray Mallee, South Australia. *South Australian Naturalist* 53: 52–58.

BROOK, A. J., 1982. *Atlas of Frogs of Victoria.* Department of Zoology, University of Melbourne, Publication No. 6: 36 pp.

BROWN, G. W., 1983. *Comparative feeding ecology of south-eastern Australian scincids.* Unpublished Ph.D. Thesis, Latrobe University, Bundoora: 1–382.

BUSTARD, R., 1970. *Australian Lizards.* Collins, Sydney-London: 162 pp.

COGGER, H. G., 1974. Thermal relations of the mallee dragon, *Amphibolurus fordi* (Lacertilia: Agamidae). *Australian Journal of Zoology* 22: 319–339.

COGGER, H. G., 1979. Reproductive cycles, fat body cycles and socio-sexual behaviour in the mallee dragon, *Amphibolurus fordi* (Lacertilia: Agamidae). *Australian Journal of Zoology* 26: 653–672.

COGGER, H. G., CAMERON, E. E. & COGGER, H. M., 1983. *Zoological Catalogue of Australia, 1, Amphibia and Reptilia.* Australian Government Publishing Service, Canberra, vi + 313 pp.

COGGER, H. G., 1992. *Reptiles & Amphibians of Australia*. Reed, Chatsworth, 774 pp.

COVENTRY, A. J. & DIXON, J. M., 1984. Small native mammals from the Chinaman Well area, North western Victoria. *Australian Journal of Mammalogy* 7: 111–115.

LITTLEJOHN, M. J., 1966. Amphibians of the Victorian Mallee. *Proceedings of the Royal Society of Victoria* 79: 605–619.

LITTLEJOHN, M. J., 1971. Amphibians, in Amphibians and Reptiles of Victoria. *Victorian Year Book* 85: 1–36.

MATHER, P. B., 1979. An examination of the Reptile Fauna of Wyperfeld National Park using Pitfall Trapping. *Victorian Naturalist* 96: 98–101.

MENKORST, P. W., 1982. Pitfall trapping for reptiles in the Big Desert, Victoria. *Victorian Naturalist* 99: 66–70.

PATCHELL, F. & SHINE, R., 1986. Food habits and reproductive biology of the Australian legless lizards (Pygopodidae). *Copeia*: 30–39.

PIANKA, E. R., 1986. *Ecology and natural history of desert lizards. Analyses of the ecological niche and community structure*. Princeton University Press, Princeton, N.J. 208 pp.

QUALLS, C. P., SHINE, R., DONNELLAN, S. & HUTCHINSON, M. 1995. The evolution of viviparity within the Australian scincid lizard *Lerista bougainvillii*. *Journal of Zoology* 237: 13–26.

RAWLINSON, P. A., 1966. Reptiles of the Victorian Mallee. *Proceedings of the Royal Society of Victoria* 79: 605–619.

RAWLINSON, P. A., 1971. Reptiles, in Amphibians and Reptiles of Victoria. *Victorian Year Book* 85: 1–36.

SHINE, R., 1977a. Reproduction in Australian Elapid Snakes. II. Female reproductive cycles. *Australian Journal of Zoology* 25: 655–666.

SHINE, R., 1977b. Reproduction in Australian Elapid Snakes. Testicular Cycles and Mating Seasons. *Australian Journal of Zoology* 25: 647–653.

SHINE, R., 1981. Venomous Snakes in Cold Climates: Ecology of the Australian Genus *Drysdalia* (Serpentes : Elapidae). *Copeia* (1): 14–25.

SPENCER, W. B., 1896. In *Report of the Horn Scientific Expedition to Central Australia* 1: 196–199, W. B. Spencer, ed., Dalau and Co., London; Melville, Mullen and Slade, Melbourne.

WITTEN, G. J. & COVENTRY, A. J., 1984. A new Lizard of the genus *Amphibolurus* (Agamidae) from Southern Australia. *Proceedings of the Royal Society of Victoria* 96 (3): 155–157.

WITTEN, G. J. & COVENTRY, A. J., 1990. Small *Pogona vitticeps* (Reptilia : Agamidae) from the Big Desert, Victoria, with notes on other *Pogona* populations. *Proceedings of the Royal Society of Victoria* 102 (3): 117–120.

REGENERATION OF HEATH AND HEATH WOODLAND IN THE NORTH-EASTERN OTWAY RANGES THREE TO TEN YEARS AFTER THE WILDFIRE OF FEBRUARY 1983

MARGARET C. WARK

Angair Incorporated (Anglesea and Aireys Inlet Society for the Protection of Flora and Fauna), PO Box 12, Anglesea, Victoria 3230

WARK, M. C., 1996:12:31. Regeneration of heath and woodland in the north-eastern Otway Ranges three to ten years after the wildfire of February 1983. *Proceedings of the Royal Society of Victoria* 108 (2): 121–142. ISSN 0035-9211.

Studies of the post-fire regeneration of the heath, tall shrubland, scrub and heath woodland communities in the Anglesea district, 3–10 years after the wildfire of 1983, show that maximum post-fire species richness of vascular plants occurred in the early years after fire, and that no additional species appeared between 3 and 10 years post-fire. Vascular plant species richness decreased with time since fire, and by year 10 was 60% of that in years 1–3. Approximately 40% herbaceous species and 80% shrub species present immediately post-fire were still present at year 10. In contrast, the species richness of non-vascular plants increased almost four-fold with time since fire. Twenty-nine additional species appeared between 3 and 10 years as canopy and understorey cover increased.

In the heath woodlands, the eucalypt canopy reached approximate pre-fire height and projective cover levels by 7 years. Recovery of the heathy substratum slowed as canopy cover increased between 3 and 10 years. Over 70% of the understorey species which remained at year 10 had the capacity to regenerate vegetatively after fire. In areas not affected by *Phytophthora cinnamomi*, sclerophyllous shrubs were the main component of the understorey at year 10.

THE north-eastern Otway Ranges, Victoria, is a species-rich region of south-eastern Australia containing extensive areas of fire-prone dry sclerophyll forest and heath woodland (Beauglehole et al. 1977; Parsons et al. 1977; Carr & Robinson 1985; Meredith 1986; Australian Heritage Commission 1993). Until 1983 there had been no published study of the fire ecology of the flora and fauna of this region. Following the wildfire of Ash Wednesday (17 February 1983) in which almost 40 000 ha of vegetation near Anglesea and Airey's Inlet were burnt, a ten year study of post-fire recovery of vegetation and fauna was initiated. This multidisciplinary project involved groups from Angair, Deakin University, the Royal Australian Ornithological Union and the Museum of Victoria, who monitored recovery in six of the major plant communities in the district (coastal heath, heath woodland, ironbark open-forest, sand dune scrub, swamp thicket and fern gully).

The aims of the botanical study were to monitor vegetation recovery following wildfire, and to provide information for use in conservation management.

Data on early stages of regeneration of coastal heath and heath woodland communities have been published (Wark et al. 1987), and key findings were:

1. *Species re-establishment*
   Ninety per cent of all species present before the fire reappeared within the first year. All other species reappeared by year 2.

2. *Regeneration strategies*
   Thirty-seven per cent of species were obligate regrowth regenerators, 30% facultative regrowth regenerators, and 33% obligate seed regenerators.

3. *Structure recovery*
   Rate of recovery of canopy height in heath woodlands (in years 1–3 post-fire) was faster than rate of recovery of canopy projective cover.

4. *Flowering response*
   Fifty-two per cent of species flowered in the first year after fire, and 98% had flowered by the end of the third year.

   Most of the species which flowered in the first year were herbaceous, and included members of the Liliaceae, Orchidaceae, Droseraceae, Asteraceae and Poaceae.

   The early 'herbaceous phase' declined in cover and density of flowering during the second and third years as shrub and canopy cover increased. Grazing by native and intro-

duced mammals reduced frequency and density of herbaceous species in the early years after fire.

5. *Seeding response*
   Though most shrubs commenced flowering within two years of fire, few had produced seed by year 3.

This present paper reports data collected in coastal heath and heath woodland 3 to 10 years after fire and examines changes which have occurred during this time. Mammal, bird and insect data have been reported separately (Wilson & Moloney 1985a, 1985b; Reilly 1985, 1991; Andersen 1987).

SITE DESCRIPTIONS

The three study sites (A, B and C) each contained several plant communities ranging from coastal closed heath (dominated by *Banksia marginata*, *Allocasuarina pusilla* and *Leptospermum myrsinoides*) to heath woodland dominated by *Eucalyptus obliqua*. They have already been described in detail (Wark et al. 1987, fig. 1, table 1) and will be referred to in the present paper as plant subcommunities at subsites. In this paper the general term 'heath woodland' will include the physiognomic types open scrub, tall shrubland and woodland. The fire history of every site differed. Site A was crown fired by wildfires in 1958 and 1983; site B was control burnt in 1973, and crown scorched by wildfire in 1983; and site C was crown fired by wildfires in 1969 and 1983 (P. Denham, pers. comm.; Cecil 1993a, 1993b).

Site C was near an operating open cut brown coal mine. Unfortunately this site was destroyed by mining operations which commenced six years post-fire. However, sites A and B remained undisturbed and data collected at these two sites up to 10 years post-fire are presented below.

Because of the extent of the Ash Wednesday wildfire (Wark et al. 1987, fig. 1), no unburnt sites comparable to sites A, B and C existed for comparison.

METHODS

Vegetation

Pre-fire data. Detailed species lists existed for vascular plants for each site prior to the 1983 fire (White 1982). However no quantitative data on pre-fire floristics or vegetation structure were available. Approximate pre-fire height was

interpreted from pre-fire photographs and the height of burnt tips. Approximate pre-fire projective cover was also estimated from pre-fire field observations and photographs.

Data collection and data analysis. For methods see Wark et al. (1987). Data were collected in spring, 3, 7 and 10 years after fire. Total species lists were made for each site and subsite at each survey, and this information used to supplement quadrat data on floristics, flowering and regeneration strategies. As in the previous paper (Wark et al. 1987), the term 'total number of species' at a site (or subsite) refers to the total number of species recorded in the quadrats *plus* any additional species recorded at that site (or subsite). In the present paper, quadrat data alone is used to analyse the relationship between plant species richness and total vascular plant cover.

Nomenclature of most plants follows Ross (1993); for *Danthonia* now *Rytidosperma* — N. Walsh, pers. comm.; for mosses — Scott & Stone (1976); liverworts — Scott (1985); lichens — Filson & Rogers (1976); and orchids — Backhouse & Jeanes (1995). Name changes of vascular plants which have occurred since the earlier paper (Wark et al. 1987) are presented in the Appendix. In addition, three species of plants were incorrectly identified in Wark et al. (1987), and will be referred to by their correct names in the present paper. They are the liverwort *Marchantia polymorpha* now known to be *Marchantia berteroana* (Scott, 1985); the fungus *Omphalia chromacea* now known to be *Gerronema postii* (May & Fuhrer, 1989); and the herb *Viola hederacea* ssp. *sieberiana* now known to be *Viola cleistogamoides*. Species of the moss *Campylopus* (especially *C. clavatus* and *C. pyriformis*) are very hard to discriminate when young, and misidentifications are to be expected.

Regeneration strategies terminology. Terminology follows Purdie (1977a, 1977b), namely: OSR = obligate seed regenerator (regenerating from seed or propagates only); FRR = facultative regrowth regenerator (regenerating by regrowth, and from seed or propagules); ORR = obligate regrowth regenerator (regenerating by regrowth only).

Other methods

Rainfall. Rainfall data for Anglesea (for years 1986–1989 inclusive) were obtained from the Bureau of Meteorology. No records were kept at Anglesea for 1990–1992, so rainfall figures

for these years are unofficial (courtesy the late P. F. Marriott).

Soil pathogens. Samples of soil $10 \times 10 \times 10$ cm taken (in October 1985) near dying plants of *Isopogon ceratophyllus* R.Br. and *Xanthorrhoea australis* R.Br. (approx. three years after fire) were tested for the presence of *Phytophthora cinnamomi* Rand by Dr G. C. Marks (Department of Conservation & Natural Resources) using a cotyledon baiting technique (Marks & Kassaby 1974).

Field observations for the continued presence of *P. cinnamomi* continued to year 10. Dying plants of *I. ceratophyllus* and *X. australis* were used to indicate the presence of *P. cinnamomi* throughout the study to year 10 (Weste & Taylor 1971; Weste & Law 1973). Sites where *P. cinnamomi* may have killed *X. australis* in the pre-fire period were indicated by the presence of burnt out stem bases of *X. australis.*

RESULTS

Soils

Moisture. Field observations between years 3 and 10 confirmed the previous observations of seasonal water logging in depressions and shallow slopes during winter (June–August). Total rainfalls for Anglesea (annual mean 657 mm) for the years 1986 to 1992 inclusive were 622, 740, 643, 825, 596, 614 and 758 mm respectively.

Soil pathogens. *Phytophthora cinnamomi* Rands was isolated from soil and root samples taken from dying plants of *I. ceratophyllus* and *X. australis* at four of the six subsites (A_2, B_1, B_2 and B_3) approximately three years post-fire. Signs of dieback due to *P. cinnamomi*, as shown by indicator species, occurred in patches as a mosaic at all subsites in the 10 years post-fire.

At four of the six subsites (A_2, B_1, B_2 and B_3) the presence of burnt out bases of *X. australis* indicated that the pathogen may have been present before the fire occurred. Such indications of pre-existing *P. cinnamomi* disease were seen upslope of, and adjacent to, all of the subsites at site B. These probable areas of infection contained few sclerophyllous shrubs and the understorey which regenerated in the ten years following the fire was sparse and open and composed mainly of sedges and rushes such as *Gahnia radula*, *Lepidosperma semiteres* and *Lepidosperma filiforme.* Dying and dead sclerophyllous shrubs and *X. australis* appeared in the heathy understorey down slope from these areas in the ten years following the fire.

Vegetation

Floristics. The floristics of the plant subcommunities one, three and ten years post-fire are presented as presence–absence data in Table 1 (data collected in year 7 have not been included but are available from Angair). Two hundred and twenty-one species of vascular plants appeared by 3 years post-fire and no additional vascular plant species between 3 and 10 years. In contrast, 10 species of non-vascular plants appeared by year 3 and an additional 29 non-vascular plant species between years 3 and 10.

A total of 6 tree species, 63 shrubs, 141 species of herbs, 5 creepers and climbers, 6 ferns and 39 species of non-vascular plants were present, giving a total species list of 260 for the ten years post-fire at sites A and B (Table 1). In this paper the term graminoid will not be used, and the term herb will be used to mean an herbaceous species (Table 3).

Total plant species richness (quadrat and site data combined) ranged from 86–159 per subcommunity (Table 1), and from 42–86 at year 10 post-fire (Table 1); a reduction of approximately 40% when compared with years 1 and 3 combined (78–137 species; Table 1).

The total number of species present 10 years post-fire was also approximately 60% of the year 1 and 3 level (Table 3). The number of herbaceous species present decreased by year 10 to about 40% of the year 1–3 level (Table 3).

Only 22% of species of Poaceae, 42% of lilies and irises, and 50% of Orchidaceae seen 1–3 years post-fire were recorded at year 10. However, 60% of species of sedges and rushes present at year 1 were still seen at year 10. In contrast, 80% of species of shrubs seen at years 1–3 were still recorded at year 10 (Table 3). Ten shrub species were present at all subsites at years 1, 3, 7 and 10. They were *Acrotriche serrulata*, *Epacris impressa*, *Leucopogon virgatus*, *Monotoca scoparia*, *Platylobium obtusangulum*, *Leptospermum myrsinoides*, *Banksia marginata*, *Isopogon ceratophyllus*, *Pimelea humilis* and *Tetratheca ciliata.*

Though non-vascular plants were uncommon, the number of species present increased three and a half-fold by year 10, compared with years 1 and 3 (Tables 1, 3; 10 species years 1–3, 35 species year 10). The early colonisers (*Funaria hygrometrica*, *Marchantia berteroana*) which appeared at year 1, were not seen after year 3. Seven additional species of bryophytes appeared between years 2 and 3, and an additional 29 species after year 3. Between years 3 and 10 post-fire, the

Site	A			B		
Subsite Vegetation formation	A₁ Closed heath	A₂ Open scrub	A₃ Tall shrubland	B₁ Woodland	B₂ Woodland	B₃ Woodland/ closed scrub
Trees*						
Myrtaceae						
Eucalyptus aromaphloia			(1) (3)(10)			
Eucalyptus baxteri		1 3 10	(1)			
Eucalyptus obliqua	(1) (3)(10)	1 3 10	1 3 10	1 3 10	3 (10)	1 3 10
Eucalyptus tricarpa		1 3 (10)	(1)			
Eucalyptus viminalis				(1) (3)(10)		
Eucalyptus willisii				(1) (3)(10)	(1) (3)(10)	(1) (3)(10)
Tall shrubs*						
Casuarinaceae						
Allocasuarina verticillata	1 3 10		1 3 10			
Mimosaceae						
Acacia pycnantha		1 3 10	(1) (3)(10)			
Acacia verticillata						1 3 10
Algae**						
Nostoc spp.	10		10			
Lichens**						
Cladia aggregata	3 10	3 10	10	10	10	10
Cladia schizopora	10					
Cladonia cervicornis ssp.			(10)	10		10
Cladonia chlorophaea	3	3		10		
Cladonia corniculata			(10)	10	10	
Cladonia praetermissa		10				
Cladonia *? merochlorophaea*		10				
Cladonia enantia	10					10
Cladonia spp.	10	10	10		10	
Parmelia spp.	10					
Ramalina spp.	10		10			
Teloschistes spp.	10					
Thysanothecium *scutellatum*						10
Usnea ? inermis	10					10
Unidentified spp.		3 10	10			
Liverworts**						
Cephaloziella exiliflora		(10)				
Chaetophyllopsis *whiteleggei*	(10)	10				
Enigmella thallina	10	(10)	10			
Fossombronia *? intestinalis*	(10)					
Goebelobryum *unguiculatum*		10			3 10	10
Hyalolepidozea *longiscypha*		10				
Kurzia compacta					10	10
Lophocolea semiteres	(10)					
Lethocolea pansa	10	(10)	10			
Marchantia berteroana		1 3				
Riccardia aequicellularis	(10)					
Fungi**						
Gerronema postii	1				(3)	

Table 1 continued next page (see legend on page 131)

Site Subsite Vegetation formation	A			B		
	A₁ Closed heath	A₂ Open scrub	A₃ Tall shrubland	B₁ Woodland	B₂ Woodland	B₃ Woodland/ closed scrub
Mosses**						
Barbula calycina	3 (10)	3 10		10	3	
Bryum argenteum		10				
Bryum billardieri	(10)				10	
Bryum pachytheca	3					
Campylopus australis					10	
Campylopus clavatus	10	10	10			
Campylopus introflexus	3 10	10	10	10	3 10	3 10
Ceratodon purpureus	3	3 (10)	3		3	3
Funaria hygrometrica	3	1 3	3		3	3
Funaria bullata	(10)		(10)			
Polytrichum commune	· 10					
Polytrichum juniperinum		10				10
Tayloria octoblepharis	10	(10)				
Unidentified spp.	3 10	3	3 10	3	3	3
Ferns and allies**						
Lindsaeaceae						
Lindsaea linearis		(3)			(3)	
Schizaeaceae						
Schizaea bifida					(3)	
Schizaea fistulosa						(1) (3)
Selaginellaceae						
Selaginella uliginosa						(1) 3 10
Centrolepidaceae						
Centrolepis aristata	1 3 10		1			
Centrolepis strigosa		(3)		(1) (3)		
Sedges and rushes**						
Cyperaceae						
Baumea acuta						(1) (3)(10)
Caustis flexuosa					(3)	
•*Cyperus tenellus*	(1) (3)				(3)	
Gahnia radula	(1) (3)(10)	1 3 10	(1) (3) 10	1 3 10	1 3 10	1 3 10
Isolepis inundata	1					
•*Isolepis marginata*	1					
Lepidosperma concavum	1 3 10	1 3 10	1 3 10			
Lepidosperma filiforme				10		
Lepidosperma semiteres	1 3 10	1 3 10	1 3 10	1 3 10	(3)	
Schoenus apogon	1 3	1 3	1 3		(3)	
Schoenus breviculmis	1 3 10	1 3 10	1 3 10	(1) (3)		
Schoenus brevifolius						(1) (3)(10)
Schoenus tenuisimus					1 3 10	1 3 10
Juncaceae						
Juncus pauciflorus		(3)				
Juncus planifolius						(1) (3)
Restionaceae						
Empodisma minus						1 3 10
Hypolaena fastigiata				(3)	1 3 10	1 3 10
Unidentified sedge/rush						10

Table 1 continued next page (see legend on page 131)

Site	A			B		
Subsite Vegetation formation	A_1 Closed heath	A_2 Open scrub	A_3 Tall shrubland	B_1 Woodland	B_2 Woodland	B_3 Woodland/ closed scrub
Grasses**						
Poaceae						
•*Aira caryophyllea*		3				
Agrostis avenacea	(3)	(3)				
Amphipogon strictus	1 3 10	1 3 10	10			
Rytidosperma caespitosum		(1)				
Rytidosperma geniculatum	(3)	(3)	1 (3)			
Rytidosperma indutum	1	1	1	(1)	(1)	
Rytidosperma pilosum		(1)	1			
Rytidosperma procerum		(1)				
Rytidosperma semiannularis		(1)				
Rytidosperma setaceum	1 3 10	1 3 10	1 3 10	1 3 10	(1)	(1)
Rytidosperma tenuis		(1)				
Deyeuxia densa						(1)
Deyeuxia quadriseta		(1)	(1)	1		(1)
Dichelachne crinita	(1)	(1)				
Dichelachne rara						(1)
•*Holcus lanatus*	(1)	(1)				
Microlaena stipoides	(1)	(1)		(1)		
Poa morrisii						1 3 (10)
Poa sieberiana		1 3 10				
Stipa semibarbata	1 3 10	1 3 10	1 3 10	1 3 10	(1)	
Tetrarrhena distichophylla		(1) (3)				
Themeda triandra		(1)				
•*Vulpia myuros*		1 3				
Unidentified grasses	1 3 10	1 3 10	1 10	1 3		1 10
Orchids**						
Orchidaceae						
Acianthus caudatus	(1)	1 (3)(10)	1 (3)		(1)	
Acianthus pusillus	1 (3)	3 (10)	3 10		(1)	
Caladenia cardiochila	(1)	1 (3)(10)		1	(1)	
Caladenia carnea	(1)				(1)	
Caladenia deformis	(1)				(1)	
Caladenia tentaculata	1 (3)	(10)	3	1 3	(1)	
Caladenia pusilla	1 3				(1)	
Caladenia spp.		(10)				(10)
Calaena major				(1)	(1) 3	
Calochilus campestris					(1)	(1)
Calochilus robertsonii					(1)	(1)
Chiloglottis reflexa					(3)	
Cyrtostylis reniformis		(3)	(3)		(1)	
Diuris corymbosa	1 (3) 10	(3)	(3)	1 (3)	(1)	
Eriochilus cucullatus	(1)				1	1 3
Glossodia major	(1) (3)	1 3 (10)		1 (3)	1 (3)	1 3
Leptoceras menziesii	(1) (3)				(1)	(1) (3)(10)
Microtis parviflora	(1)	(10)	1			
Microtis uniflora	1	(1)				
Orthoceras strictum	(1)		1	(1)	(1)	

Table 1 continued next page (see legend on page 131)

Site	A			B		
Subsite Vegetation formation	A₁ Closed heath	A₂ Open scrub	A₃ Tall shrubland	B₁ Woodland	B₂ Woodland	B₃ Woodland/ closed scrub
Orchids** *(continued)*						
Orchidaceae *(continued)*						
Genoplesium despectans					(1)	
Prasophyllum elatum					(1)	
Genoplesium morrisii	1 (3)	(3)(10)	1 (3)		(1)	
Prasophyllum odoratum	1				(1)	
Pterostylis longifolia	(1)	(1) (3)	10		(1)	
Pterostylis nana	(3)	(3)	1 (10)		(1)	
Pterostylis nutans		(1)				
Pterostylis parviflora	1 (3)	(3)	1	1 10	(1)	
Pterostylis plumosa	1 (3)	(10)	3 10	3 10		
Pterostylis sanguinea		(10)				
Pyrorchis nigricans				1 3 10	1 3	
Thelymitra antennifera	1 3 (10)	3 10	3 10	1 (3) 10	1	(3)
Thelymitra flexuosa	(3)		3	(1)		
Thelymitra benthamiana	(1) (3)		(1) (3)(10)			
Thelymitra ixioides	(3)	3	1	(1)	(1)	
Thelymitra pauciflora	1	10		1 3	(1)	
Thelymitra rubra	1 (3)			(3)	(1)	3
Thelymitra spp.	1 3 (10)	3 (10)	1 3	1 10		(10)
Lilies and irises**						
Liliaceae						
Burchardia umbellata	1 3 10	1 3 10	1 3 10	1	1 3 10	
Caesia parviflora	1 3					3
Chamaescilla corymbosa	1 3 10	1 10	1 10			3 10
Dianella revoluta		(1) (3)		(1) (3)	(1) (3)	
Arthropodium strictum	(1)	(1)				
Laxmannia orientalis	1 3	1 3	1 3 10	1 3 10	1 3 10	1 3 (10)
Lomandra filiformis	(1) (3)(10)	1 3	1 3 10	1 3	(1) 3 10	1 3 10
Lomandra longifolia					1 3 10	
Lomandra micrantha		(1) (3)				
Lomandra multiflora		(3)	1			10
Thysanotus juncifolius	(1) 3	(1)				
Thysanotus patersonii	1 3 (10)	1 3 10	1 3	1 3 10	1	(10)
Thysanotus tuberosus	(1)	(1)			1	
Wurmbea dioica	(1)	(1)				
Xanthorrhoeaceae						
Xanthorrhoea australis		1 3 10	10	(1) (3)(10)	1 3 10	1 3 10
Xanthorrhoea minor						(1) (3)(10)
Hypoxidaceae						
Hypoxis glabella		(1)			(1)	
Iridaceae						
Patersonia fragilis	(1) (3)	(1) (3)				1 3
Patersonia occidentalis		(1) (3)				1 3
Shrubs**						
Mimosaceae						
Acacia verticillata var. ovoidea						(1) (3)(10)
Acacia myrtifolia		(1) (3)(10)			(1) (3)(10)	
Acacia suaveolens				1 3 10	(1) (3)(10)	

Table 1 continued next page (see legend on page 131)

Site	A			B		
Subsite Vegetation formation	A₁ Closed heath	A₂ Open scrub	A₃ Tall shrubland	B₁ Woodland	B₂ Woodland	B₃ Woodland/ closed scrub
Shrubs (continued)						
Epacridaceae						
Acrotriche serrulata	1 3 10	(1) 3 10	(1) 3 10	1 3 10	(1) 3 10	1 3 10
Astroloma humifusum	1 3 10	10		(3)		
Brachyloma ciliatum				(1) (3)		
Epacris impressa	1 3 10	1 3 10	1 3 10	1 3 10	1 3 10	1 3 10
Lissanthe strigosa			(1) (3)			
Leucopogon australis						(1) (3)(10)
Leucopogon virgatus	1 3 10	1 3 10	1 3 10	(1) 3 10	1 3 10	(1) 3 10
Monotoca scoparia	1 3	1 3	(1) 3 (10)	(1) (3)	1 3 10	(1) 3 10
Sprengelia incarnata						1 3 (10)
Fabaceae						
Aotus ericoides					1 3 10	(1) 3
Bossiaea prostrata	3					
Daviesia brevifolia	(3)	(3)	(3)			
Dillwynia glaberrima				(1) (3) 10	1 3 10	1 3 10
Dillwynia hispida	(3)(10)	(3)(10)	1 3 10			
Dillwynia sericea	1 3 10	1 3 (10)	1 3 10	1 3		
Gompholobium ecostatum	1 3 10	1 3 10	1 3 10	1 3 10		
Hovea linearis		(3)	1 3 10	1 3 10		
Platylobium obtusangulum	1 3 10	1 3 10	1 3 10	1 3 10	(1) (3)	1 3 10
Pultenaea daphnoides		(1) (3) 10				
Pultenaea dentata			(3)			
Pultenaea gunnii					(3)	
Pultenaea humilis	(1) (3)	(1) (3)	(1) 3			
Pultenaea mollis			3			
Pultenaea stricta						(3)(10)
Sphaerolobium vimineum	3 10	(3)				3 10
Myrtaceae						
Baeckea ramosissima ssp. prostrata	3	(3) 10				
Leptospermum continentale	10	3 10	10	(3)(10)		1 3 10
Leptospermum myrsinoides	1 3 10	1 3 10	1 3 10	1 3 10	1 3 10	1 3 10
Melaleuca squarrosa						1 3 10
Proteaceae						
Banksia marginata	1 3 10	3 10	3 10	(1) (3)(10)	1 3 10	1 3 10
Hakea ulicina		(3)(10)		(3)(10)		
Isopogon ceratophyllus	1 3 10	1 3 10	1 3 10	(1) (3)(10)	1 3 10	(1) 3 10
Lomatia ilicifolia		(1) (3)	(1) (3)(10)		(1) (3)	
Persoonia juniperinum		(1) (3)(10)		1 3 10	1 3 10	1 3 10
Rutaceae						
Correa reflexa			(1) (3)(10)			
Casuarinaceae						
Allocasuarina pusilla	1 3 10	(1) (3)	1 3 10	(1) (3)(10)		1 3 10
Polygalaceae						
Comesperma ericinum						(1) 3

Table 1 continued next page (see legend on page 131)

Site	A			B		
Subsite Vegetation formation	A_1 Closed heath	A_2 Open scrub	A_3 Tall shrubland	B_1 Woodland	B_2 Woodland	B_3 Woodland/ closed scrub
Shrubs** *(continued)*						
Rhamnaceae						
Cryptandra tomentosa	(1) 3 (10)		(1) 3 (10)	(1) 3 10		
Spyridium parvifolium		(1) 3 (10)		10		
Spyridium vexilliferum	1 3 10	1 3 10	1 3 10			
Dilleniaceae						
Hibbertia prostrata				(1) (3)	1 3 10	1 3 10
Hibbertia sericea	10	(1) (3)	1 3	10		
Hibbertia riparia	1 3 10	(1) 3 10	(1) 3 10	1 3 (10)		
Hibbertia stricta	1 3 10	(1) 3 10	(1) 3 10	1 3 (10)		
Sterculiaceae						
Lasiopetalum baueri		(10)	(1) (3)(10)			
Thomasia petalocalyx		(10)	1 (3)(10)			
Asteraceae						
Olearia erubescens					(1) (3)	
Olearia myrsinoides					(1) (3)	
Olearia ramulosa		(1) (3)				
Olearia teretifolia	1 3 10	1 3 (10)	1 3 10			
Thymelaeaceae						
Pimelea glauca		(3)				
Pimelea humilis	1 3 10	1 3 10	1 3 10	(1) (3)	1 3 10	1 3
Pimelea linifolia		(3)(10)				
Pimelea octophylla	(1) (3)	(1) (3)	(1) 3	(1) (3)		
Pimelea phylicoides	3 10	3				
Solanaceae						
Solanum laciniatum		(1) (3)				
Tremandraceae						
Tetratheca ciliata	1 3 10	(1) (3)(10)	3 10	(3)(10)	1 3 10	3 10
Herbs**						
Rosaceae						
Acaena novae-zelandiae		(1) (3)				
Asteraceae						
Brachyscome uliginosa	1 3 (10)	3 (10)	1 3			
Craspedia spp.		(1) (3)			(1) (3)	
Argentipallium *obtusifolium*	(1) (3)	(1) (3)	(1) 3	(10)	(3)	(1) 3
Helichrysum scorpioides		(3)		3 (10)	(3)	3
Ixodia achillaeoides		(1) 3				
Lagenifera gracilis				1		(1)
Leptorhynchos *squamatus*		(1)				
Euchiton sphaericus		(3)				
Euchiton involucratus		(3)				
Euchiton spp.		10				
Euphorbiaceae						
Amperea xiphoclada						1 3
Poranthera microphylla				10		1

Table 1 continued next page (see legend on page 131)

Site	A			B		
Subsite / Vegetation formation	A₁ Closed heath	A₂ Open scrub	A₃ Tall shrubland	B₁ Woodland	B₂ Woodland	B₃ Woodland/ closed scrub
Herbs ** (*continued*)						
Droseraceae						
Drosera peltata ssp. *auriculata*	1 3 10	3 10	1 3 10	1 3 10	1 3 10	1 3 10
Drosera glanduligera	1 3 (10)	3 10		(1) (3)(10)	1 3	
Drosera macrantha	1 3 10	(3) 10	3 10	1 3 10	1 10	10
Drosera peltata	1	3			1 3	1 3
Drosera pygmaea	1 3				10	1 3 10
Drosera whittakerii	1	3 10		1 10	1 3 10	1 3 10
Rubiaceae						
Galium binifolium						(3)
Galium gaudichaudii						(3)
Opercularia scabrida				3 10		
Opercularia varia	1 3 10	1 3 10	1 3 10	1 3 10	1 3	1 3 10
Haloragaceae						
Gonocarpus tetragynus	1 3 10	1 3 10	1 3 10	1 3 10	1 3 10	1 3 10
Gonocarpus micranthus						(3) 10
Goodeniaceae						
Goodenia geniculata	1 3 10	1 3 10	1 3 10	1 3 10		(3)(10)
Goodenia lanata		(1) (3)	10	1	1 3	1 3 10
Scaveola albida	(3)		(3)			
Umbelliferae						
Hydrocotyle callicarpa		(3)	1	1		(3)
Hydrocotyle sibthorpioides						(3)
Platysace heterophylla				1 3	1 3 10	1 3
Xanthosia pusilla	1 3 10	3	1 3 10	1 3 10	1 3 10	1 3 10
Xanthosia dissecta						(3)
Lobeliaceae						
Lobelia gibbosa					(1)	(1) (3)
Lobelia rhombifolia	10	(3)			(3)	
Loganiaceae						
Mitrasacme pilosa						(3) 10
Oxalidaceae						
Oxalis corniculata		(3)				
Plantaginaceae						
Plantago varia		(1) (3)				
Stackhousiaceae						
Stackhousia monogyna	(1)	(1) (3)				
Stylidiaceae						
Stylidium graminifolium	(1) 3				(1) 3	
Stylidium perpusillum					(10)	
Violaceae						
Viola cleistogamoides	1 3 10	3 (10)	3 10			
Campanulaceae						
Wahlenbergia gracilenta	(1)	(1)		1 3		
Wahlenbergia stricta	(1)			1 10	1	
Polygalaceae						
Comesperma calymega	1 3	3	3	3	1 3	1 3 10
Geraniaceae						
Pelargonium australe	1			10		

Table 1 continued next page (see legend on page 131)

Site	A			B		
Subsite Vegetation formation	A_1 Closed heath	A_2 Open scrub	A_3 Tall shrubland	B_1 Woodland	B_2 Woodland	B_3 Woodland/ closed scrub
Herbs (*continued*)						
Brunoniaceae						
Brunonia australis		(1)			(1)	
Creepers and climbers						
Pittosporaceae						
Billardiera scandens		(1) 3	1 3			1 3 10
Lauraceae						
Cassytha glabella	1 (3) 10	1 3 (10)	1 3 10	3 10	1 3 10	3 10
Cassytha melantha		(3)(10)				
Polygalaceae						
Comesperma volubile	1 3 10					
Fabaceae						
Kennedia prostrata	1	(1) 3 10			3	
Seedlings						
Monocotyledon	1	1	1	1	1	1
Dicotyledon	1	1 10	1	1	1	1
Sub-total vascular species in quadrats Year 1, Year 3, Year 10	64, 53, 43	38, 56, 42	49, 53, 46	42, 37, 38	38, 37, 29	40, 53, 39
Sub-total additional vascular species at site Year 1, Year 3, Year 10	31, 27, 8	51, 54, 26	19, 17, 10	24, 24, 14	42, 21, 5	24, 20, 15
Total vascular species[†] Year 1, Year 3, Year 10	95, 80, 51	89,110, 68	58, 70, 56	66, 61, 52	80, 58, 34	64, 73, 54
Sub-total non-vascular species in quadrats Year 1, Year 3, Year 10	1, 7, 16	2, 6, 13	0, 2, 7	0, 1, 6	0, 5, 8	0, 3, 9
Sub-total additional non-vascular species at site Year 1, Year 3, Year 10	0, 0, 7	0, 0, 5	0, 0, 3	0, 0, 0	0, 1, 0	0, 0, 0
Total non-vascular species[†] Year 1, Year 3, Year 10	1, 7, 23	2, 6, 18	0, 2, 10	0, 1, 6	0, 6, 8	0, 3, 9
Total species[†] Year 1, Year 3, Year 10	96, 87, 74	91,116, 86	68, 72, 66	66, 62, 58	80, 64, 42	64, 76, 56
Total species[†] Years 1–3 combined	115	137	86	78	99	84
Total species[†] Years 1–10 combined	136	159	100	86	103	96
Total species[†] Years 1–10 combined	260 species 221 species vascular plants 39 species non-vascular plants					

Table 1. Floristic comparisons between subsites 1, 3 and 10 years after fire. *Key:* 1 = present in quadrats year 1; 3 = present in quadrats year 3; 10 = present in quadrats year 10; (1) = present at site year 1; (3) = present at site year 3; (10) = present at site year 10; *11 × 12 m quadrats; **1 × 2 m quadrats; [†] = total species present in quadrats plus additional species present at site.

number of species of lichens present increased from 2 to 14 (Table 1).

In general, the number of non-vascular plant species increased with time since fire, while the number of vascular plant species decreased with time since fire (Tables 1, 3, Fig. 5).

Structure.   The structure of the plant communities post-fire is presented in Table 2 and Figs 1–5. (In this paper the term 'shrub stratum' or understorey will also include the ground stratum.)

(a) E. obliqua *canopy recovery post-fire.*   At all heath woodland sites, the rate of recovery of projective cover of the overstorey (relative to approximate pre-fire projective cover) accelerated between years 3 and 7 (Fig. 3). By year 7 the *E. obliqua* canopy of most heath woodland communities had reached both approximate pre-fire height and approximate pre-fire projective cover levels (Fig. 3).

Death of some basal, trunk and crown epicormic regrowth of *E. obliqua* occurred in all heath wood-land communities as canopy recovery progressed (cf. profiles figs 3c, d, 4c, d of Wark et al. 1987; and Figs 1, 2 of this paper). In scrub, shrubland and woodland, whole epicormics died between 3 and 7 years, possibly from water stress or *P. cinnamomi* infection. In scrub and shrubland, shedding and death of large basal and trunk epicormics were often observed between 3 and 7 years. In these coastal communities, at least twice between 3 and 7 years, young regrowth tips on the seaward side of *E. obliqua* were killed by what appeared to be chloride toxicity from salt-laden winds.

(b) Shrub stratum (understorey) recovery post-fire.   By year 7, the projective cover of the shrub stratum of all coastal (site A) subcommunities had reached approximate pre-fire levels (Table 2); in contrast, height of the shrub stratum in exposed locations had reached only 70–80% of the approximate pre-fire levels by year 7, and remained at about this level till year 10 (Table 2).

Subsite Vegetation type	A₁ Closed heath	A₂ Open scrub	A₃ Tall shrubland	B₁ Woodland	B₂ Woodland	B₃ Woodland/ closed scrub
Eucalypts (species)	—	EO**	EO	EO	EO	EO
Cover (%)						
Pre-fire (approx.)	—	30–70	10–30	10–30	10–30	10–30
3 years	—	20	20	20	20	20
7 years	—	70	30	30	30	30
10 years	—	70	30	30	30	30
Height (m)						
Pre-fire (approx.)	—	4.4	2.5	11.7	11.8	10.4
Live stem height after fire						
(year 0)	—	3.0	0.4	8.5	9.0	7.5
3 years	—	3.7	2.2	10.7	10.3	8.7
7 years	—	3.5	3.0	11.0	11.0	9.0
10 years	—	4.3	3.5	11.1	11.1	9.4
Understorey						
Cover (%)						
Pre-fire (approx.) all plants	70–100	30–70	30–70	30–70	30–70	30–70
3 years	64	61	57	20	75	92
7 years	92	75	76	37	78	76
10 years all plants	98	78	81	57	70	88
Height (m)						
Pre-fire (approx.)	0.5	1.0	0.5	0.5	1.5	1.5
Live stem height after fire						
(year 0)	0.0	0.0	0.0	0.0	0.0	0.0
3 years	0.2	0.2	0.2	0.2	1.0	0.8
7 years	0.35	1.0	0.31	0.7	1.0	1.0
10 years	0.35	1.0	0.35	0.8	1.1	1.2

Table 2.   Structure of plant communities 3, 7 and 10 years after fire. *Tallest stratum; **EO = *Eucalyptus obliqua.*
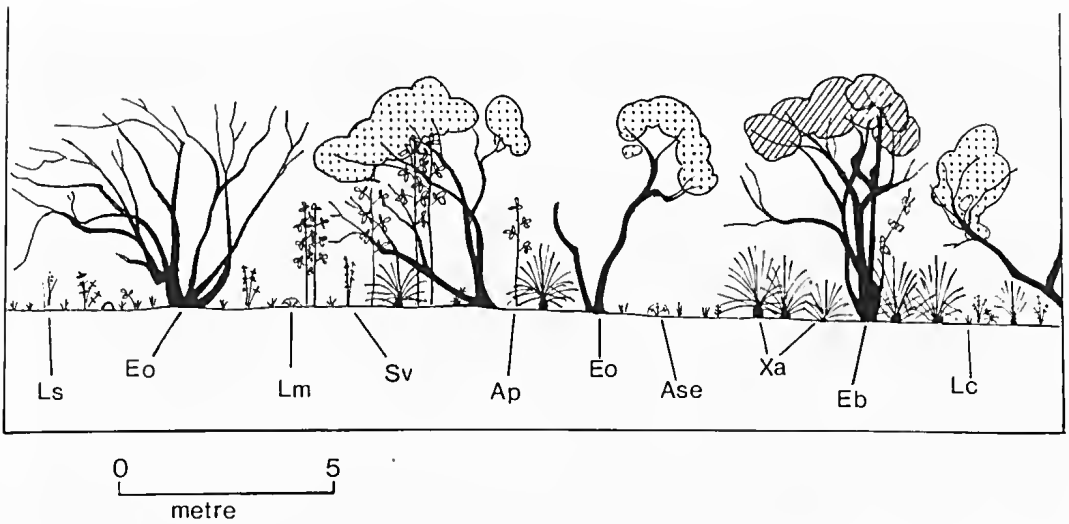
Fig. 1. Vegetation profile in open scrub (subsite A$_2$) 10 years after fire. Horizontal and vertical axes are the same. Stippling and hatching indicates the extent of canopy regrowth. (Profiles immediately after fire and at 3 years are shown in Wark et al. 1987 — fig. 3c, d.) Eo = *Eucalyptus obliqua*, Eb = *Eucalyptus baxteri*, Xa = *Xanthorrhoea australis*, Ls = *Lepidosperma semiteres*, Ac = *Acacia pycnantha*, Ase = *Acrotriche serrulata*, Lm = *Leptospermum myrsinoides*, Sv = *Spyridium vexilliferum*, Lc = *Lepidosperma concavum*.
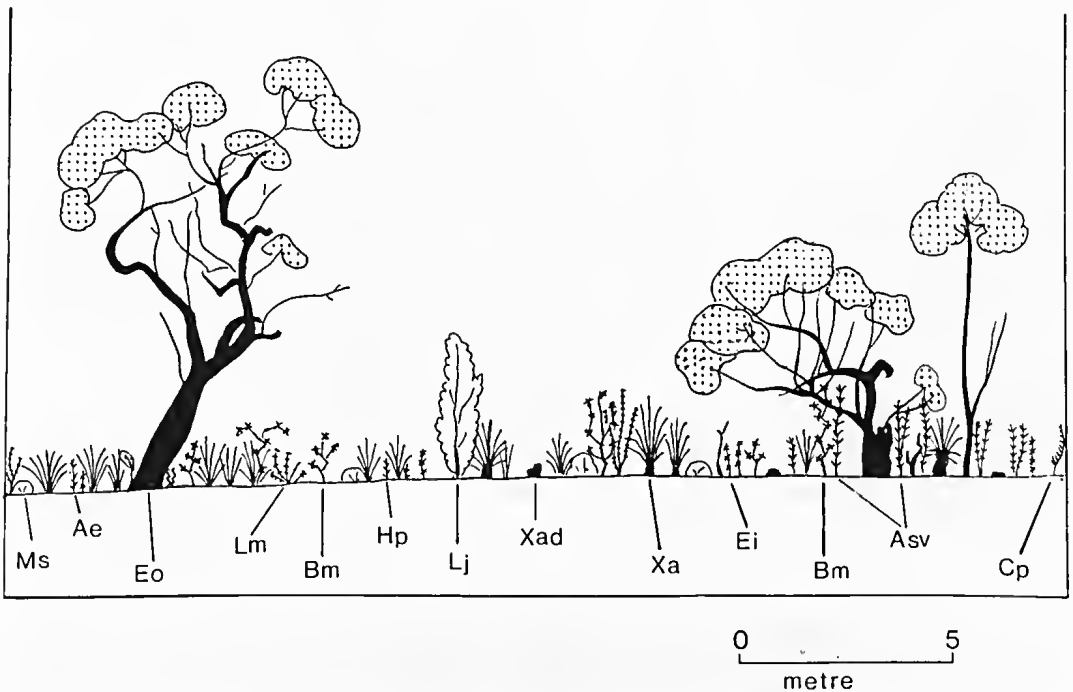

Fig. 2. Vegetation profile in woodland (subsite B$_2$) 10 years after fire. (Profiles immediately after fire and at 3 years are shown in Wark et al. 1987 — fig. 4c, d.) Eo = *Eucalyptus obliqua*, Xa = *Xanthorrhoea australis*, Xad = dead *Xanthorrhoea australis*, Lm = *Leptospermum myrsinoides*, Bm = *Banksia marginata*, Ms = *Monotoca scoparia*, Ei = *Epacris impressa*, Ae = *Aotus ericoides*, Hp = *Hibbertia prostrata*, Lj = *Leptospermum continentalis*, Asv = *Acacia suaveolens*, Cp = *Allocasuarina pusilla*.

At site B, shrub stratum height had reached 91% of its approximate pre-fire level by year 7 (Table 2), and by year 10 both height and projective cover had reached approximate pre-fire levels (Table 2).

(c) Cover of shrub stratum 1–10 years post-fire.   In both closed heath and heath woodland, cover of all herbs in the shrub stratum (other than sedges, rushes and *X. australis*) never exceeded 1% during the ten years post-fire. Shrubs were the major component of both closed heath, and the heath woodland understorey from year 3 onwards (Fig. 4).

A litter layer, composed of canopy-derived material (including shed branches and dead epicormic regrowth), plus shrub layer litter (including plants possibly killed by competition, water stress or *P. cinnamomi*) developed in the heath woodlands from year 3 onwards (Fig. 4). Where signs of *P. cinnamomi* dieback were seen, dead plants of *X. australis* and dead sclerophyllous shrubs were often a major component of the litter layer (cf. profiles fig. 4c, d, Wark et al. 1987; and Fig. 2 of this paper).

(d) Vascular plant cover and species richness 1–10 years post-fire.   In both closed heath and heath woodland, the total number of species of vascular plants (in quadrats) decreased, and the total number of species of non-vascular plants (n quadrats) decreased as the combined percentage cover of the canopy and understorey increased (Fig. 5; Tables 1–3).

Bryophyte cover on the soil surface increased 3–10 years post-fire as the percentage of bare ground decreased and shrub cover increased. By year 10, bryophyte cover was 5% and 2% of total substratum cover in closed heath and heath woodlands respectively (Fig. 4).

Regeneration strategies

Approximately 70% of all species present at 1–3 years post-fire, and still remaining 10 years post-fire, had regenerated vegetatively after fire (Table 3). Half of the shrubs regenerating post-fire were sprouters and regenerated from lignotubers or rootstocks (Tables 1, 3; Wark et al. 1987, table 4). The other half of the shrubs established
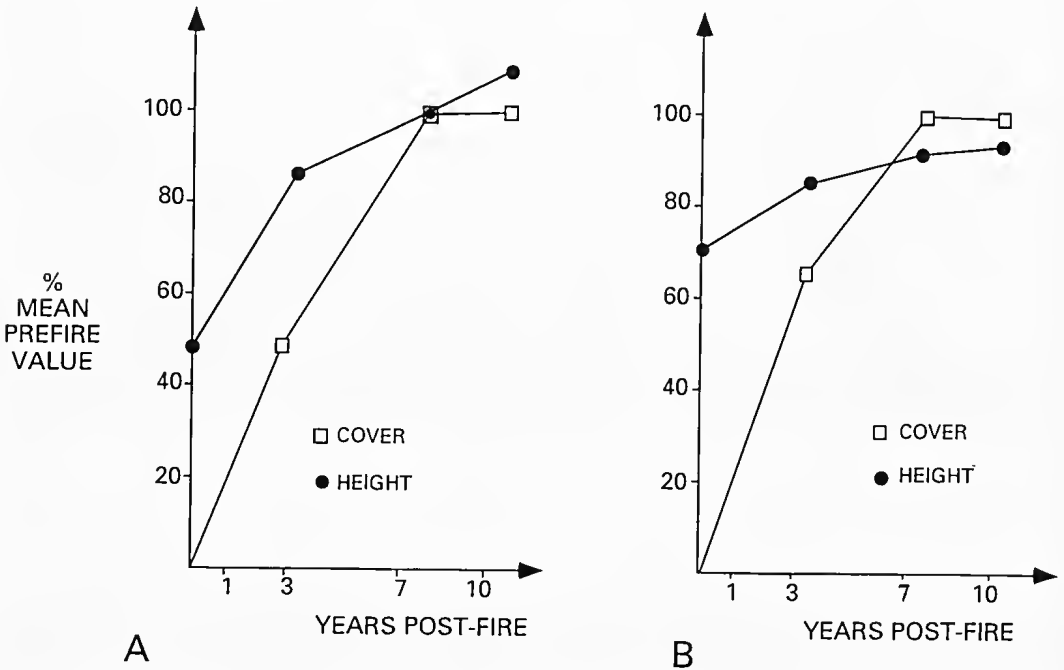

Fig. 3.   Eucalyptus obliqua canopy recovery in heath woodland communities years 1–10 post-fire.   A, Site A, subsites A₂ and A₃ combined.   B, Site B, subsites B₁, B₂ and B₃ combined.

from seed, 1–2 years post-fire. By year 10, 51% of FRR shrubs remained compared with 44% of OSR shrubs. Seven of the 10 species of shrubs present at all sites at years 1, 3, 7 and 10 were FRR species (*A. serrulata*, *L. virgatus*, *L. myrsinoides*, *M. scoparia*, *P. obtusangulum*, *B. marginata* and *I. ceratophyllus*).

Ninety-eight per cent of the monocotyledonous herb species appearing post-fire were also sprouters (72% ORR and 26% FRR). ORR species included all sedges and rushes, all orchids and most lilies and irises. FRR species included 87% of grasses, the lilies *X. australis* and *X. minor*, and the irises *Patersonia fragilis* and *P. occidentalis*. Regrowth of both ORR and FRR species was by sprouting from rhizomes, stolons, corms or tubers.

Half of the dicotyledonous herb species appearing post-fire were ORR or FRR sprouters and the other half obligate seed regenerators.

In both cases, less than half these species survived till year 10.

Few obligate seed regenerators became major components of the shrub (or tall shrub) stratum by year 10. Exceptions were *Acacia pycnantha*, *Olearia teretifolia* and *Spyridium vexilliferum* at site A; and *Acacia myrtifolia*, *A. suaveolens*, *A. verticillata*, *Spyridium parvifolium* and *Sprengelia incarnata* at site B.

Few seedlings of tree, shrub or herbaceous species were observed 7 and 10 years post-fire. The massive seedling germination seen in the first two years post-fire never recurred in later years. Seedling densities decreased as the amount of bare ground decreased (Fig. 6). By year 10, seedling densities of *Spyridium vexilliferum* and *Epacris impressa* in closed heath had reduced to <0.1% of the year 1 level (132/m², 138/m² — Wark et al. 1987), and only 1–2 mature plants survived per m².
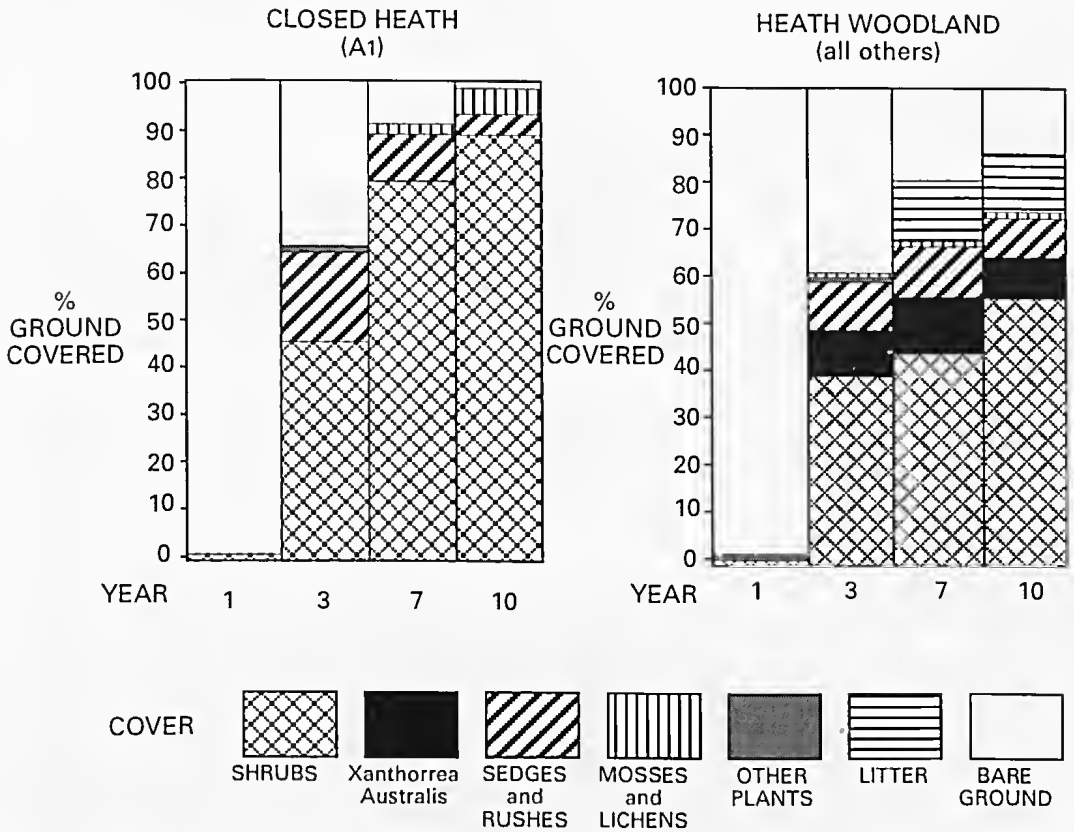

Fig. 4. Projective cover of shrub stratum in closed heath and heath woodland communities 1, 3, 7 and 10 years post-fire (closed heath = subsite A₁; heath woodland = subsites A₂, A₃, B₁, B₂ and B₃ combined).
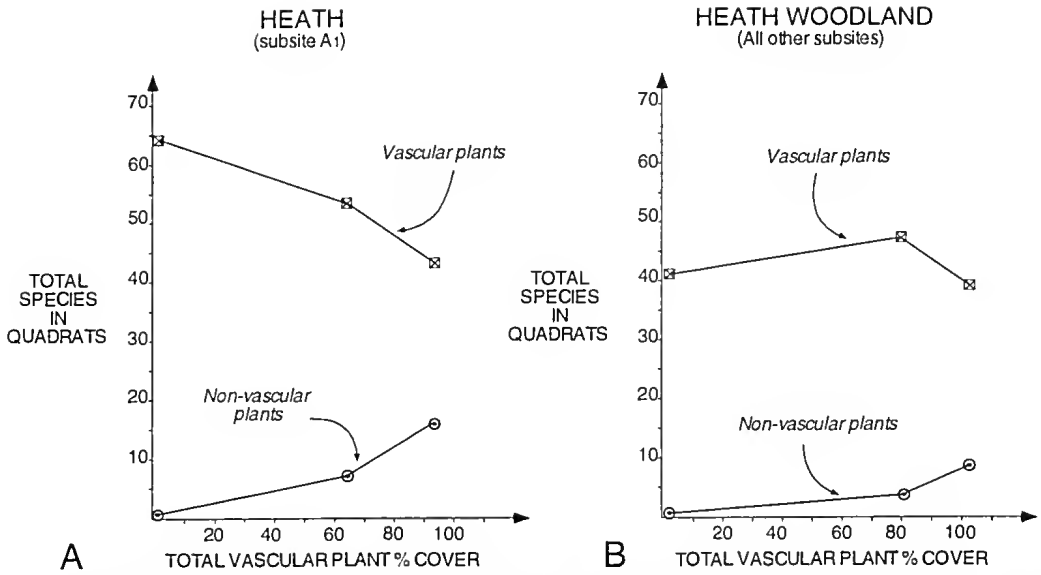
Fig. 5. Relationship of species richness to total vascular plant % cover. A, Closed heath = subsite A₁. B, Heath woodland = subsites A₂, A₃, B₁, B₂ and B₃ combined. *Note:* Heath woodland 'total vascular plant % cover' = total canopy and total understorey vascular plant % cover *combined*, minus litter layer cover.

Species present Regeneration strategy post fire	Years 1–3			Year 10		
	OSR	FRR	ORR	OSR	FRR	ORR
Trees (6)*	—	6	—	—	6	—
Shrubs (63)	32	31	—	21	27	—
Dicotyledon herbs (46)	23	12	11	13	4	7
Monocotyledon herbs (95)						
Orchids (36)	—	—	36	—	—	18
Lilies and irises (19)	—	4	15	—	2	6
Grasses (23)	3	20	—	—	5	—
Sedges and rushes (17)	—	—	17	—	—	10
Creepers and climbers (5)	5	—	—	5	—	—
Ferns (6)	—	2	4	—	1	1
Non-vascular plants (10)†	10	—	—	5	—	—
Sub-total	73	75	83	44	45	42
Total species‡ (%)	32	32	36	34	34	32
Total species‡†		231			131	

Table 3. Regeneration strategies and life form groups of all species appearing 1–3 years post fire, and still present 10 years post fire. *Key:* OSR = obligate seed regenerators; FRR = facultative regrowth regenerators; ORR = obligate regrowth regenerators. Terminology follows Purdie (1977a, b). *Note:* *Numbers in brackets show total species present years 1–3; †29 species (mosses, lichens, liverworts, algae) which appeared after year 3, and were present at year 10, have not been included in these data; ‡Total species = total number of species recorded (quadrat and site data combined).

When young *E. impressa* seedlings were found at year 10, these were always in open areas (e.g. along access tracks near the study sites, where there was probably less competition for light, moisture and nutrients).

Seedling densities of *Eucalyptus obliqua* in closed heath remained unchanged at 5/ha between years 3 and 10 post-fire (5/ha—years 3 and 10). In contrast, year 10 *E. obliqua* seedling densities in open scrub were 1% of the year 3 level (>1000/ha year 3, cf. <10/ha year 10).

Flowering response after fire

The frequency of flowering of orchids decreased between years 1 and 10. Only 50% of the 34 species of orchids which appeared and flowered at year 1 were both present and flowered at year 10 (Table 1). A similar reduction occurred in the number of species of lilies and irises flowering at year 10 (42% of year 1 level).

All species of eucalypts and shrubs which had not flowered and set seed by year 3 flowered and set seed by year 7. Shrubs included the obligate seeder *Hakea ulicina*.

DISCUSSION AND CONCLUSIONS

Species richness post-fire

The species richness of vascular plants in heath and heath woodland decreased with time post-fire, as reported for other heath and heath woodland communities in Australia (Specht et al. 1958; Russell & Parsons 1978; Posamentier et al. 1981; Specht 1981; Bell et al. 1984; McFarland 1988; Specht 1994).

There was both a floristic change and an increase in the number of species of non-vascular plants with time. The early post-fire moss and liverwort colonisers (*Funaria hygrometrica*, *Marchantia berteroana*) appeared in the first year, as part of a succession (Wark et al. 1987) and were not seen after 3 years. Similar observations have been made by Cremer and Mount (1965) and Duncan & Dalton (1982) in Australian sclerophyll forests. With the exception of *F. hygrometrica* (Southorn 1976, 1977), the factors which promote post-fire colonisation of dry sclerophyll forests by bryophytes are not well understood (Warcup 1981). In the present study, the number of species of non-vascular plants present increased as vascular plant cover increased. Two species were observed at year 1; by year 3 (when understorey total plant cover was 60–65% of pre-fire) an additional 7 species (mainly mosses) had been recorded; and

by year 10 (when understorey total plant cover was 87–98% of pre-fire) an additional 29 species (mainly lichens) were found. It is probable that several species of lichens were present earlier, but because of their slow growth rate were not recognised. Most of the lichens identified at year 10 were decay species. Most of the liverworts identified at year 10 were ground or wood species which require some shade and moisture; their presence may indicate changed climatic and edaphic conditions in the ground stratum by year 10.

Vegetation structure post-fire

It was observed from year 3 onwards that, as canopy cover of the overstorey increased, species richness of the heathy substratum declined and shrubs became increasingly dominant, as reported for other heath woodlands in Australia (Specht et al. 1958; Russell & Parsons 1977; Specht & Specht 1989).

The rate of recovery of canopy height and cover was faster than that of the substratum, as reported for other heath woodlands in southern Australia (Specht & Morgan 1981). Canopy recovery may be influenced by a variety of factors such as the presence of *P. cinnamomi*, moisture stress, or exposure to salt wind. Canopy dieback has already been reported for the Anglesea area (Weste 1975) and death of regenerating *E. obliqua* canopy at sites A and B, between 3 and 7 years post-fire, could have been caused by *P. cinnamomi* which was isolated from soil at both sites. In early years post-fire, damage observed on both canopy and heathy understorey at site A was probably caused by salt spray (Wark et al. 1987). Similar effects have been described by Parsons and Gill (1968) and Parsons (1979) for other coastal heathlands in Australia, and may explain the slow recovery of height of the open scrub canopy and the closed heath substratum at Point Addis.

The post-fire regeneration strategies of the Anglesea heaths and heath woodland communities conform to the 'initial floristic composition' regeneration model (Egler 1954; Purdie & Slatyer 1976). All species of vascular plants known to be present prior to the fire re-established during the first three years post-fire (White 1982; Wark et al. 1987) and no additional species appeared between 3 and 10 years post-fire.

Vegetative regrowth is the main regeneration strategy after fire in the Anglesea heaths and heath woodlands (Wark et al. 1987). Seventy per cent of all species that survived the first 10 years

post-fire were either FRS or ORS sprouters as reported for other heaths and dry sclerophyll woodlands in southern Australia (Gill & Groves 1979; Specht 1981). Most sprouting species appeared before those which regcnerated from seed, with the competitive advantage of established root systems, in areas of limited water, nutrients or light.

Seedling mortality was high in the early years post-fire (Wark et al. 1987; present study) and few seedlings established once regrowth commenced; this same pattern was recorded for Dark lsland heath South Australia (Specht et al. 1958). Both Specht (1981) and Gill (1981) have observed that seedling regeneration in southern Australian heaths was restricted to the immediate post-fire period. ln the present study, it was noted that once regrowth of sprouting species became vigorous, there was high mortality of seedlings which had established in gaps. Competition for space, water, nutrients and light all probably contributed to this increased mortality.

Some obligate seeders (e.g. *Hakea ulicina*) did not set seed in the first 3 years after fire, and it was suggested that burning of the heaths and heath woodlands within the first 3 years could result in elimination of such species (Wark et al. 1987). Coaldrake (1951) observed elimination of the OSR shrub *Banksia ornata* from South Australian heaths burnt twice within 3 years, and Gill and McMahon (1986) estimated that a 16 year fire-free interval could be needed to achieve stand replacement of this fire-sensitive species.

In the prescnt study, it was observed that all obligate seeders had set seed by ycar 7 post-fire. It could be assumed that burning of the Anglesea heaths and heath woodlands 7 ycars or more after fire would probably not eliminate OSR regenerators such as *H. ulicina*. However, recent demographic studies in New South Wales on the OSR shrubs *Banksia ericifolia* and *Petrophile pulchella* show that freedom from fire during the primary juvenile period is only one of several factors which influence successful establishment of fire-sensitive OSR species (Bradstock & O'Connell 1988).

The success of seedling establishment (which may be affected by climate, predation, or rate of seed relcase post-firc), thc size of the pre-fire seed bank and the rate of survival of seedlings, juveniles and adults, may also influence post-fire survival of OSR species. Bradstock and O'Connell (1988) have shown that, although *B. ericifolia* sets seed 6 years post-fire, if seedling establishment rates are low post-fire, a fire-free interval of 13 years is required to ensure population replacement.

More information is needed on the life cycles and demographic behaviour of the fire-sensitive OSR species of the Anglesea–Airey's Inlet heaths and heath woodlands to assist in conservation management.

Flowering response post-fire

The spectacular post-fire flowering response of herbaceous species which occurred in the first year post-fire (Wark et al. 1987), was not seen in later years. Similar observations have been made by Gill (1981, 1993) and Specht (1981, 1994) for a range of heath woodlands in Australia. ln the present study, species of the families Liliaceae and Orchidaceae appeared, but often did not flower between 3 and 10 years post-fire. The lack of flowering may be due to lack of light or moisture, or to the absence of a fire stimulus such as the presence of extra nutrients which accumulate in ash, or originate from the humus layer.

Phytophthora cinnamomi

Phytophthora cinnamomi was isolated from the Anglesea area in 1973 prior to the fire, and from all sites 3 years after the 1983 firc. Thc early isolations in this area (by Dr G. Marks) were from sitcs as widespread as the lron Bark Basin Reserve, Point Addis; the Ocean Road Flora Reserve, Anglesea; and the Angahook State Park, Airey's lnlet (Weste & Marks 1974; Weste 1975; Pittaway 1976).

lt appears that *P. cinnamomi* disease may have been present at most of the subsites prior to the 1983 wildfire. Symptoms and mortalities in susccptible specics indicated disease extension from all subsites during the first decade after fire. Specics were replaced by resistant sedges and rushes, which may act as tcmporary reservoirs of infection (Phillips & Weste 1984).

lt is possible that *P. cinnamomi* disease is modi-fying the vegetation floristics of the Anglesea area. ln the Brisbane Ranges, Grampians and Wilson's Promontory National Parks, *P. cinnamomi* die-back has resulted in the transformation of a species-rich heath woodland community to a sedge-woodland containing few species (Weste & Taylor 1971; Weste & Law 1973; Weste 1981, 1986; Kennedy & Weste 1986). Such changes have been observed in the Ocean Road Flora Reserve, east of Anglesea, where *P. cinnamomi* has modified the floristics and caused changes in cover and local reduction in species richness (Weste & Marks 1974; Weste 1975). Similar changes may be occurring at site B in the present

study (Wark et al. 1987), in the coastal heath and heath woodlands west of Anglesea (Carr et al. 1991), in the Angahook–Lorne State Park (Carr et al. 1995a) and in the heath woodlands of the Alcoa leasehold north of Anglesea (Meredith 1986; Cameron & Downe 1994; Carr et al. 1995b).

A recent study of vegetation changes associated with *P. cinnamomi* invasion in the Grampians National Park has produced quantitative evidence that *P. cinnamomi* disease may threaten the survival of rare, susceptible endemic species (Kennedy & Weste 1986) . The distribution of the pathogen in the Anglesea area is currently patchy (G. Weste, pers. comm.), however wider spread could threaten local endemics such as *Grevillea infecunda*, which only occurs in a few scattered patches near Anglesea. This is an obligate re-sprouter (Wark et al. 1987) which never reproduces from seed (McGillvray 1993). *P. cinnamomi* disease could result in its elimination. *Conospermum mitchelli* and *Hakea repullulans* are two other ORR shrubs which though not endemic could be threatened by *P. cinnamomi* disease spread. Investigations are needed to determine whether these 3 species are susceptible and whether they grow in areas currently or likely to become infested. The latter can only be determined when the precise distribution of *P. cinnamomi* in the Anglesea area is known.

Management practices are required to control *P. cinnamomi* disease spread in the Anglesea–Airey's Inlet region, particularly with regard to road construction, the use of infested gravel, and the cleaning of road vehicles.

ACKNOWLEDGEMENTS

REFERENCES

ANDERSEN, A., 1987. A survey of the invertebrates of the Anglesea region following wildfire. Report to Angair Inc.

AUSTRALIAN HERITAGE COMMISSION, 1993. Anglesea Heath/Bald Hills Area. Entry on the Register of the National Estate (unpublished).

BACKHOUSE, G. & JEANES, J., 1995. *The Orchids of Victoria*. Melbourne University Press, Carlton.

BEAUGLEHOLE, A. C., CARR, G. W. & PARSONS, R. F., 1977. A floristic check list of the Otway region, Victoria. *Proceedings of the Royal Society of Victoria* 89: 99–122.

BELL, D. T., HOPKINS, A. J. M. & PATE, J. S., 1984. Fire in the Kwongan. In *Kwongan Plant Life of the Sandplain*, J. S. Pate & J. S. Beard, eds, University of Western Australia Press, Nedlands.

BRADSTOCK, R. A. & O'CONNELL, M. A., 1988. Demog-raphy of woody plants in relation to fire: *Banksia ericifolia* L.f. and *Petrophile pulchella* (Schrad) R.Br. *Australian Journal of Ecology* 13: 505–518.

CAMERON, D. G. & DOWNE, J. M., 1994. Assessment of an area adjacent to the Anglesea Heath/Bald Hills area. Report to the Australian Heritage Commission, Flora Section, Flora, Fauna & Fisheries Division, Department of Conservation & National Resources.

CARR, G. W. & ROBINSON, R. W., 1985. Vegetation of the Anglesea/Airey's Inlet area and its significance. Submission to the Land Conservation Council Melbourne Study Area, District 1 Review, 1985.

CARR, G. W., PEAKE, P. & WARD, L. A., 1995a. Flora and fauna surveys, Angahook–Lorne State Park, Victoria: rare plants, vegetation communities and vertebrate fauna of selected sites. Report prepared for Department of Conservation & Natural Resources (August 1995).

CARR, G. W., MCMAHON, A. R. G., BEDGOOD, S. E. & TODD, J. A., 1991. The vegetation. In *An assessment of the flora and fauna of O'Donohues land, Anglesea, Victoria*, Biosis Research Pty Ltd, eds, report prepared for Gerner Sanderson Pty Ltd (August 1991).

CARR, G. W., MUIR, A. M., PEAKE, P. & WARD, L. A., 1995b. Flora, fauna and biological significance of the Mt Ingoldsby section of the Alcoa Anglesea Lease Area, Victoria. Report to Alcoa Australia Limited (September 1995).

CECIL, K. L., 1993a. *The Red Steer—Bushfires along the Great Ocean Road*, Vol. 1. Anglesea District Historic Society, Anglesea.

CECIL, K. L., 1993b. *The Red Steer—Bushfires along the Great Ocean Road*, Vol. II. Anglesea District Historic Society, Anglesea.

COALDRAKE, J. E., 1951. Ecology of part of the Ninety-mile Plain, South Australia. CSIRO (Aust.) Bulletin, No. 283, 138 pp.

CREMER, K. W. & MOUNT, A. B., 1965. Early stages of plant succession following the complete felling and burning of *Eucalyptus regnans* forest in the Florentine Valley, Tasmania. *Australian Journal of Botany* 13: 303–319.

DUNCAN, D. & DALTON, P. J., 1982. Recolonisation by bryophytes following fire. *Journal of Bryology* 12: 53–63.

EGLER, F. E., 1954. Vegetation science concepts. 1. Initial floristic composition, a factor in old field vegetation development. *Vegetatio* 4: 412–417.

FILSON, R. B. & ROGERS, R. W., 1976. *Lichens of South Australia*, S.A. Government Printer, Adelaide.

FORBES, S. J., GULLAN, P. K., KILGOUR, R. A. & POWELL, M. A., 1984. *A Census of the Vascular Plants of Victoria*, 3rd edn, National Herbarium of Victoria, South Yarra.

GILL, A. M., 1981. Adaptive responses of Australian vascular plant species to fires. In *Fire and the Australian Biota*, A. M. Gill, R. H. Groves & I. R. Noble, eds, Australian Academy of Science, Canberra, 243–272.

GILL, A. M., 1993. Interplay of Victoria's flora with fire. In *Flora of Victoria*, Vol. 1, *Introduction*, D. B. Foreman & N. G. Walsh, eds, Inkata Press, Melbourne, 212–226.

GILL, A. M. & GROVES, R. H., 1981. Fire regimes in heathlands and their plant ecological effects. In *Ecosystems of the World*, Vol. 9B, *Heathlands and Related Shrublands*, R. L. Specht, ed., Elsevier, Amsterdam, 61–84.

GILL, A. M. & McMAHON, A. 1986. A post-fire chronosequence of cone, follicle and seed production in *Banksia ornata. Australian Journal of Botany* 34: 425–433.

GILL, A. M., MOORE, P. H. R. & MARTIN, W. K., 1994. *Bibliography of Fire Ecology in Australia (including Fire Science and Fire Management)*, Edition 4, NSW National Parks & Wildfire Service, Hurstville.

KENNEDY, J. & WESTE, G., 1986. Vegetation changes associated with invasion by *Phytophthora cinnamomi* on monitored sites in the Grampians, western Victoria. *Australian Journal of Botany* 34: 251–279.

MARKS, G. & KASSABY, F. Y., 1974. Detection of *Phytophthora cinnamomi* in soils. *Australian Forestry* 36: 198–203.

MAY, T. & FUHRER, B., 1989. Notes on fungi occurring after fire in Australia. Introduction and description of *Gerronema postii. Victorian Naturalist* 106: 133–137.

McFARLAND, D. C., 1988. Fire and the vegetation composition and structure of subtropical heathlands in south-eastern Queensland. *Australian Journal of Botany* 36: 533–546.

McGILLIVRAY, D. J., 1993. *Grevillea (Proteaceae)—a Taxonomic Revision*. Melbourne University Press, Carlton.

MEREDITH, C. W. 1986. *The vegetation of the Anglesea Lease Area*. Report to the Land Conservation Council of Victoria, Melbourne.

PARSONS, R. F., 1979. Salt spray effects in heathlands. In *Ecosystems of the World*, Vol. 9B, *Heathlands and Related Shrublands*, R. L. Specht, cd., Elsevier, Amsterdam, 225–230.

PARSONS, R. F. & GILL, A. M., 1968. The effects of salt spray on coastal vegetation at Wilson's Promontory, Victoria, Australia. *Proceedings of the Royal Society of Victoria* 81: 1–9.

PARSONS, R. F., KIRKPATRICK, J. B. & CARR, G. W., 1977. Native vegetation of the Otway region. *Proceedings of the Royal Society of Victoria* 89: 77–88.

PHILLIPS, D. & WESTE, G., 1984. Field resistance in three native monocotyledon species that colonise indigenous sclerophyll forest after invasion by *Phytophthora cinnamomi. Australian Journal of Botany* 32: 339–352.

PITTAWAY, P. A., 1976. A field study of *Phytophthora cinnamomi*-associated die-back in the eastern Otway Ranges, Victoria. B.Sc.(Hons.) thesis, Department of Botany, LaTrobe University, Victoria.

POSAMENTIER, H. G., CLARK, S. S., HAIN, D. L. & RECHER, H. F., 1981. Succession following wildfire in coastal heathland (Nadgee Nature Reserve, N.S.W.). *Australian Journal of Ecology* 6: 165–175.

PURDIE, R. W., 1977a. Early stages of regeneration after burning in dry sclerophyll vegetation. 1. Regeneration of the understorey by vegetative means. *Australian Journal of Botany* 25: 21–34.

PURDIE, R. W., 1977b. Early stages of regeneration after burning in dry sclerophyll vegetation. 2. Regeneration by seed germination. *Australian Journal of Botany* 25: 35–46.

PURDIE, R. W. & SLATYER, R. O., 1976. Vegetation succession after fire in sclerophyll woodland communities in south-eastern Australia. *Australian Journal of Ecology* 1: 223–236.

REILLY, P., 1985. Vic. Group—Regeneration survey. *Royal Australian Ornithological Union Newsletter*, No. 64, p. 8.

REILLY, P., 1991. The effect of wildfire on bush bird populations in six Victorian coastal habitats. *Corella* 15: 134–142.

ROSS, J. H. (ed.), 1993. *A Census of the Vascular Plants of Victoria*, 4th edn, National Herbarium of Victoria, South Yarra, plus update bulletins Nos 4.1, 4.2, 4.3.

RUSSELL, R. P. & PARSONS, R. F., 1978. Effect of time since fire on heath floristics at Wilson's Promontory, southern Australia. *Australian Journal of Botany* 26: 53–61.

SCOTT, G. A.M ., 1985. *Southern Australian Liverworts*, Aust. Flora and Fauna Series No. 2, Bureau of Flora and Fauna, AGPS, Canberra.

SCOTT, G. A. M. & STONE, I. G., 1976. *The Mosses of Southern Australia*, Academic Press, London.

SOUTHORN, A. L. D., 1976. Bryophyte recolonisation of burnt ground with particular reference to *Funaria hygrometrica*. 1. Factors affecting the pattern of recolonisation. *Journal of Bryology* 9: 63–80.

SOUTHORN, A. L. D., 1977. Bryophyte recolonisation of burnt ground with particular reference to *Funaria hygrometrica*. 11. The nutrient requirements of *Funaria hygrometrica. Journal of Bryology* 9: 361–373.

SPECHT, R. L., 1981. Responses to fires of heathlands and related shrublands. In *Fire and the Australian Biota*, A. M. Gill, R. H. Groves & I. R. Noble, eds, Australian Academy of Science, Canberra, 395–416.

SPECHT, R. L., 1994. Major vegetation types—heathlands. In *Australian Vegetation*, R. H. Groves, ed., Cambridge University Press, Cambridge, 321–344.

SPECHT, R. L. & MORGAN, D. G. 1981. The balance between foliage projective covers of overstorey and understorey strata in Australian vegetation. *Australian Journal of Ecology* 6: 193–202.

SPECHT, R. L. & SPECHT, A., 1989. Species richness of sclerophyll (heathy) plant communities in Australia—the influence of overstorey cover. *Australian Journal of Botany* 37: 337–350.

SPECHT, R. L., RAYSON, P. & JACKSON, M. E., 1958. Dark Island heath (Ninety-Mile Plain, South Australia), VI. Pyric Succession: changes in composition, coverage, dry weight, and mineral nutrient status. *Australian Journal of Botany* 6: 59–88.

WARCUP, J. H., 1981. Effect of fire on the soil microflora and other non vascular plants. In *Fire and the Australian Biota*, A. M. Gill, R. H. Groves & I. R. Noble, eds, Australian Academy of Science, Canberra, 204–214.

WARK, M. C., WHITE, M. D., ROBERTSON, D. J. & MARRIOT, P. F., 1987. Regeneration of heath and heath woodland in the north-eastern Otway Ranges following the wildfire of February 1983. *Proceedings of the Royal Society of Victoria* 99: 41–88.

WESTE, G. M., 1975. Coastal reserves—their value and vulnerability. *Victorian Resources* 17: 29–51.

WESTE, G., 1981. Changes in the vegetation of sclerophyll shrubby woodland associated with invasion by *Phytophthora cinnamomi. Australian Journal of Botany* 29: 261–276.

WESTE, G., 1986. Vegetation changes associated with invasion by *Phytophthora cinnamomi* of defined plots in the Brisbane Ranges, Victoria, 1975–1985. *Australian Journal of Botany* 34: 633–648.

WESTE, G. M. & TAYLOR, P., 1971. Invasion of native forest by *Phytophthora cinnamomi*. 1. Brisbane Ranges, Victoria. *Australian Journal of Botany* 19: 281–294.

WESTE, G. & LAW, C., 1973. The invasion of native forest by *Phytophthora cinnamomi*. 111. Threat to the National Park, Wilson's Promontory, Victoria. *Australian Journal of Botany* 21: 31–51.

WESTE, G. & MARKS, G., 1974. Conservation of our landscape—invasion by disease. *Victorian Resources* 16: 13–15.

WHITE, M. D., 1982. Anglesea–Airey's Inlet native plant list. *In Anglesea—a Natural History Study*, 5th edn, Angair Inc., Anglesea.

WILSON, B. A. & MOLONEY, D. J., 1985a. Small mammals in the Anglesea–Airey's Inlet area of Southern Victoria—a post fire study. *Victorian Naturalist* 102: 65–70.

WILSON, B. A. & MOLONEY, D. J., 1985b. An investigation of small mammal recolonisation and vegetation regeneration in fire affected areas of the Anglesea–Airey's Inlet region. Report to the Ministry of Conservation, Forests and Lands, Victoria.

| | Authority | |
	Forbes (1984) etc.*	Ross (1993) etc.†
Trees	*Eucalyptus sideroxylon*	*Eucalyptus tricarpa*
Tall shrubs	*Casuarina stricta*	*Allocasuarina verticillata*
Sedges and rushes	*Caustis restiaceae*	*Caustis flexuosa*
Grasses	*Danthonia caespitosa*	*Rytidosperma caespitosum*
	Danthonia geniculata	*Rytidosperma geniculatum*
	Danthonia induta	*Rytidosperma indutum*
	Danthonia pilosa	*Rytidosperma pilosum*
	Danthonia procera	*Rytidosperma procerum*
	Danthonia semiannularis	*Rytidosperma semiannularis*
	Danthonia setacea	*Rytidosperma setacum*
	Danthonia tenuoir	*Rytidosperma tenuis*
	Themeda australis	*Themeda triandra*
Orchids	*Acianthus exertus*	*Acianthus pusillus*
	Caladenia menziesii	*Leptocerus menziesii*
	Caladenia dilatata	*Caladenia tentaculata*
	Diuris longifolia	*Diuris corymbosa*
	Lyperanthus nigricans	*Pyrorchis nigricans*
	Prasophyllum despectans	*Genoplesium despectans*
	Prasophyllum morisii	*Genoplesium morrisii*
	Pterostylis vittata	*Pterostylis sanguinea*
	Thelymitra fusco-lutea	*Thelymitra benthamiana*
Lilies and irises	*Dichopogon strictum*	*Arthropodium strictum*
	Laxmannia sessiliflora	*Laxmannia orientalis*
Shrubs	*Leptospermum juniperinum*	*Leptospermum continentale*
	Casuarina pusilla	*Allocasuarina pusilla*
	Hibbertia stricta	*Hibbertia stricta*
		Hibbertia riparia
Herbs	*Acaena anserinifolia*	*Acaena novae-zelandiae*
	Brachycome uliginosa	*Brachyscome uliginosa*
	Craspedia glauca	*Craspedia* spp.
	Helichrysum obtusifolium	*Argentipallium obtusifolium*
	Gnaphalium sphaericum	*Euchiton sphaericus*
	Gnaphalium involucratum	*Euchiton involucratus*
	Gnaphalium spp.	*Euchiton* spp.
	Drosera auriculata	*Drosera peltata* ssp. *auriculata*
	Scaevola pallida	*Scaevola albida*

Appendix.   Nomenclature of vascular plants—name changes since the first paper in this series.
*Forbes (1984) and other authorities listed in Wark et al. (1987); †Ross (1993) and other authorities listed in the present paper.

TRANSACTIONS

OF THE

ROYAL SOCIETY OF VICTORIA

J. E. CUMMINS OBE, MEMORIAL ORATION

PREFACE

Our Society, and the Sciences Club before us have been well served by our Cummins Memorial Orators, and this year's Orator, John Stocker, has maintained the expected high standard in the finest of styles.

Dr Stocker is a well-tempered scientist—using here the metallurgical sense of the phrase. A Melbourne medical graduate, his career was forged overseas in private-sector research, and then quenched/reheated as the first Chief Executive of CSIRO to be appointed from outside the Organisation.

Serving two masters, one heirarchical and one political, and looking after a flock which ranged from cooperative to recalcitrant in the face of change, must have honed his skills in many ways. It certainly will have taught him to think-through his public statements, and to make sure they are soundly-based. This is very much to our benefit, as will be seen when you read the printed version of his Oration.

Life now, as Director of Research and Innovation for Pratt Industries, must seem somewhat less tempestuous than it was during the previous half-decade. Again we are the beneficiaries, because less time spent putting out fires has meant more time to think in depth about Australia's future.

Lastly, for those readers who were not present for the oration on 18 July 1996, the title of his talk is made clear at the end. *Lucy's Choice* is a far-sighted paper; and it will be of real assistance to those who have a part of Australia's destiny in their hands.

J. E. CUMMINS

The inaugural Oration of the Sciences Club took place in 1974, the Orator being Sir Louis Matheson. Thus a tradition was begun which has continued each year without interruption until the present time.

In 1989, following the death of J. E. Cummins OBE, the title of the Oration was changed to the J. E. Cummins OBE Memorial Oration to honour the man who was principally responsible for the erection of the National Science Centre which was completed in 1967.

In the early 1960s the idea was conceived within the CSIRO in which J. E. Cummins was a senior scientist, of a building which would house Scientific, Technological and Learned Societies at a reasonable rental. It was envisaged that the Centre would provide the opportunity for the interchange of ideas and a furtherance of knowledge.

J. E. Cummins (Jack as he was known), was personally responsible for raising most of the funds to build the National Science Centre, known also as Clunies Ross House. He approached many individuals and large and small corporations both here and overseas and his success can be judged from the fact that, when completed, the building was free of debt.

It was Jack who conceived the idea that Clunies Ross House should contain a venue where members of various Scientific and Technological Societies could meet in an informal manner. Thus it was that The Sciences Club became the social centre of Clunies Ross House.

Jack became the inaugural President of The Sciences Club in 1968. He was appointed to the Board of Governors of Clunies Ross House in 1971, retiring in the year of his death.

A change in the philosophy of the Board of Governors in the late 1980s resulted in The Sciences Club vacating Clunies Ross House in July 1990 and merging with the Royal Society of Victoria on 1 January 1991.

It is sad to reflect on the disintegration and demise of such a wonderful and idealistic concept. The Scientific, Technological and Learned Societies are once more scattered throughout Melbourne and the National Science Centre at 191 Royal Parade, Parkville has been partly demolished and redesigned as an apartment block.

MARGARET C. HARRIS
President of The Sciences Club 1990–1991

ROYAL SOCIETY OF VICTORIA

1996 J. E. CUMMINS ORATION

18 July 1996

Delivered by DR JOHN W. STOCKER FTS FRACP

LUCY'S CHOICE

President of the Royal Society of Victoria, Max Lay, Federal Minister for Science, Peter McGauran, Council Members, distinguished guests,

I am pleased to deliver the 1996 J. E. Cummins Oration of the Royal Society of Victoria, a body whose history reaches to the gold rush times. Here in the capital city of the gold rush state, 150 years on, I wish to think with you about resources — what will be the gold lode of the coming century?

There is no doubt that it must be people — not 'knowledge' or 'information' which for me represent abstractions that defy the grasp, but people who can use these as tools to build a great and prosperous society. As an industrial research manager, as Chief Executive of CSIRO for five eventful years but most of all as father of two teenage daughters, I've had much occasion to think about the human resources we will need to secure for Australia this new 'rush of gold'.

Fellows of that 'other' royal society, the Royal Society of London, had no doubt about what it would take from Australia's earliest days. Erasmus Darwin, grandfather of Charles and a celebrated poet and polymath of his day acclaimed thus in 1790 the glorious prospects which he envisioned for the infant nation:

> *'Here future Newtons shall explore the skies.*
> *Here future Priestleys, future Wedgwoods*
> *rise'*

In invoking Sir Isaac Newton, one of the greatest mathematical minds of any age, and Joseph Priestley, the brilliant freethinker and chemist, Erasmus was clearly prophesying a future for Australia as an empire of the intellect. The odd man out in his exemplary triumvirate might appear to be the industrialist, Josiah Wedgwood, founder of the famous pottery dynasty.

But in some ways Erasmus, writing more than two hundred years ago, saw Australia's needs more clearly than many people since. We shall return to Josiah Wedgwood later.

When HMS *Beagle* called at Sydney in 1836, her young naturalist Charles Darwin was at first inspired by what he saw: 'ancient Rome, in her imperial grandeur, would not have been ashamed of such a colony,' he enthused, even going so far as to rate the settlement among the 100 wonders of the world. But as Darwin explored further into Sydney society and surrounding NSW his view became more jaundiced. Finally he concluded that the depauperate landscape and frequent droughts would preclude substantial agricultural development, and the colony would have to draw its sustenance from commerce and manufacturing industry.

History might have proved Darwin wrong in respect of agricultural development — but history has a funny habit of confounding even the most self-evident of observations. It may be that, at the dawn of the 21st Century it is poised to do so once again.

The world of the coming century in which Australia will find itself enmeshed will be perilous and challenging in ways which make the great issues of the 20th Century seem modest.

In the past half century, the central issue of the human destiny has been whether we would ruin civilisation with fearsome weapons of mass destruction.

In the coming century, the issue will be whether humanity consumes, pollutes and populates itself into crisis.

Human numbers are marching inexorably towards 8.5 billion by 2020, more than 10 billion by the middle of the century. Virtually all this growth will take place in the poorest countries and in the most fragile regions ecologically.

Merely to feed this many people at the most basic level will require the production of an additional 800 million tonnes of grain and 50 million tonnes more fish.

Yet 40 per cent of the world's croplands are already degraded, along with a quarter of its forests and its pastures, while in the oceans, the last great source of food, the global fish catch is in decline.

World demand for fresh water is rising at twice the rate of population growth, disputes between nations and ethnic groups over water are likely to lead to conflict and even to outright war.

Even the atmosphere and climate are at risk. Today the world burns 3.5 billion tonnes of coal.

But by 2050, China *alone* plans to burn 5.5 billion tonnes. While human numbers are set to double, economic activity—including the use of energy and water—is forecast to rise fivefold.

Despite the great advances in food production and medicine of the past thirty years, 800 million people still go to bed hungry, 1.3 billion remain abjectly poor, and 400 children die from malnutrition-related disease every fifteen minutes.

A world in which so many are hungry and lack even the basic essentials for a healthy and productive life is an unstable world. This instability, as the world's leading military analysts are already recognising, cannot be quarantined to a few, impoverished regions. It will spill over to affect everyone on earth—in food prices, national security, tidal movements of refugees, epidemic disease, disruptions to trade and economic growth, and the progressive undermining of the earth's life support systems of soil, air, water and biodiversity.

As US journalist Robert Kaplan puts it: 'it is time to recognise the environment for what it is ... *The* national security issue of the 21st Century'.

These are the stark realities with which today's young Australians will have to contend as they make their way in the 21st Century. The question I wish to address tonight is 'how well are we equipping them for the challenge?'.

There is no doubt that humanity is embarking on a new age, call it what you will—post-industrial, post-modern, the information age. An era that will rival and dwarf the previous revolutions in metallurgy, agriculture and industrialisation.

The defining context of this new age is that, for the first time, human wants and needs are coming into direct collision with the earth's capacity to supply them.

Until recently most human development strategies were predicated upon the assumption that there would always be an unlimited supply of resources—of food, minerals, arable soil, clean freshwater, timber, energy. It is becoming evident that this no longer holds true.

Australia is the offspring of the resources era, when there was always a patch of untilled earth, an unexploited forest or fishery, an untapped oil reserve or mineral deposit. Our economy has been largely shaped by such discoveries and, equipped with new technologies, there is little reason why we should not continue to add to them for another century or so.

But we need to ask ourselves, very carefully, whether it is wise to depend predominantly on such resources, when the rest of the world is moving along a different path.

We are on the threshold of a different time. One in which material resources are ever more scarce, but in which human resources are ever more abundant—intellect, creativity, inventiveness.

Ake Anderson of the Swedish Institute for Future Studies calls this revolution 'The C-Society', because in his view it will be dominated by communication, cognitive capacity, creativity and competitiveness.

These, he argues, are the qualities which will define who wins and who loses in the rough-and-tumble world of the 21st Century.

Already the new allegiances on which this society is forming are becoming clear. For the past 200 years the world has been demarcated into nation states. But the carefully-drawn map of the globe with which we grew up, with its fastidiously-ruled borders and colourfully-tinted countries is a fiction. It no longer exists, save in the minds of cartographers. It does not mark those places where anarchy has already swept away all semblance of government, where ancient tribal loyalties have resurfaced with a vengeance. It does not mark the new cities, the huge, festering shanty towns where cocaine and the AK47 are the only law. It does not mark the new axes of development which leap across borders, cultures, political and religious beliefs, or the network of businesses, small, medium and large which now spans the globe.

It is in these new corridors, corridors marked by ideas which travel along optic fibre cables at the speed of light, where the next human revolution is unfolding.

Snaking across England, from Cambridge in the east through Stanstead and Reading to Bath in the west is such a wellspring of 21st Century creativity—a wellspring of new ideas, technologies, dynamic young companies with high tech solutions to serious problems. I am a director of one of these—Cambridge Antibody Technology—and I love the bustle of ideas which are its very marketable asset.

Another begins on the western fringe of Tokyo, and unwinds through Osaka, Kyoto, Kobe and Nara, then leaps across to Seoul and on into China, through Shanghai, Hang Zhou and Guangzhou.

A third spears up the heart of Europe, from Basel in Switzerland, through Karlsruhe, Heidelberg and Stuttgart and on across the Baltic into Gottenburg and Stockholm.

A fourth is born in San Francisco, slips down the west coast of California picking up L.A., Orange Country, San Diego and Tijuana in Mexico.

I've had the good luck to have had some involvement with all of these.

And along these corridors flow the ideas, discoveries, new technologies and minds which are building the 21st Century. You won't find them marked on any map, because they exist only in the photo-electronic ether. They are great webs which consist of universities and private laboratories, foundations, corporations large and small, alliances which bond and dissolve as opportunities come and go. They are fountainheads of prosperity and advancement.

What sets them apart from the other regions of the world, and even from their own immediate hinterland is a sense of urgency, of striving—to discover, to create, to compete, to succeed.

These ambitions are strong enough to overcome any political, religious, ethnic or nationalistic obstacles. Those who have the vision force their way into the network. Those who lack it are fated to become the provincial backwaters, the outlands of the 21st Century.

Where Australia sits in this emerging complexity is not easy to define. In certain fields such as medicine, agricultural and environmental science we are a part of it, but in most areas we are at the periphery, an onlooker rather than a participant. We are the hostages of our history: two hundred years of belief that resources, rather than knowledge, are our greatest asset. What Donald Horne bitingly termed the 'lucky country' mentality.

How this has paid off for us in recent times is plain to see. For 28 of the past 30 years, this country has traded at a loss. Between 1980 and 1995, for example, Australia Inc. lost more than $200 billion on the balance of current account. Over roughly the same period Taiwan, a country also of 18 million people, made a profit of $250 billion. No wonder *The Economist* magazine last year described us as combining 'a third world economy with a first world standard of living'.

One of the chief reasons for our poor performance is the fact that we have on the whole persisted in the export of products which are simple and cheap, while importing those which are sophisticated and expensive—a fact which Barry Jones was rubbing our noses in more than a decade ago and which I am pleased to see Minister McGauran picking up in recent statements.

We have also, in 15 years, managed to lift national debt from under $20 billion to more than $185 billion—a point at which it takes virtually the entire earnings of our agricultural sector, for example, just to service the interest charges.

The consequence of this has been a fire-sale of Australian heirlooms and to overseas buyers— from Vegemite, Minties and Arnott's biscuits to the Age, Qantas, insurance firms, urban real estate, power and water authorities. Not many people seem to grasp the significance of the fact that Australia can now no longer afford to own its own assets.

One of the reasons for this is to be found in the Nobel prizewinning writings of two economists, Paul Romer and Robert Solow, who argued that the secret ingredient of high performing nations was not capital or manpower—but innovation. It was not *what* you knew that was important, so much as what you *did* with the knowledge. This doctrine is known as new growth theory, and though it was discovered almost 20 years ago, has yet to make much impression on Australian economic thought.

Yet you only have to look at Australia in the context of the Asia-Pacific. At a time when virtually every other country, no matter how poor or underdeveloped to begin with, is making its way up the ladder of world living standards, we have fallen from fourth place to 22nd. We have now been overtaken in GDP per capita by Japan, Singapore and Hong Kong, according to the World Bank.

And yet Australia is far more richly endowed in its ability to gain knowledge than most other countries of our region. We have one of the world's highest levels of public sector investment in science. Our researchers, especially in areas such as medicine, astronomy, agriculture and biology have an impact on world knowledge out of all proportion to their numbers and resources. Our scientific efficiency is rated very high.

Despite some fall-off in recent times, we are training new scientists and engineers at a rate faster than most OECD countries.

So what is wrong with us?

The answer is that we are not very good at realising the *value* of the knowledge which we generate.

Nor are we very good at turning that valuable knowledge into commercial and economic success.

A recent study by the Bureau of Industry Economics noted that while our science system performs strongly in world terms, the links between it and industry are still perilously weak.

Private sector investment in R&D is far below the average for either the OECD or newly-industrialising countries. Business investment in our universities, for example, is almost negligible.

As a consequence, many of our best ideas and our best researchers are driven offshore to develop

and commercialise their discoveries. The venture capital and risk taking mentality simply does not exist in this country to support them.

This is acutely ironical, considering that Australians risk—and lose—around $10 billion every year on slow horses or dogs and cunning poker machines.

This reluctance of Australians to gamble on their own brains, but rather on everything else including two flies crawling up a wall, is a dangerous national condition as we enter an age when the ability to exploit intellect and creativity will be decisive.

At the start of my speech I referred to the English potter Josiah Wedgwood, a man whom Erasmus Darwin put on an equal footing to one of the greatest mathematicians and one of the greatest chemists of all time, as the sort of person needed to inhabit and lead the new country of Australia.

Jos Wedgwood suffered an attack of smallpox as a child which led to his leg being amputated. His disability, however, proved one of his greatest advantages, because it led his enquiring mind into many important insights and discoveries. Jos Wedgwood was not merely a farsighted industrialist, he was also a scientist, a technologist, a gifted artist whose products graced the tables of the royal palaces of Europe as well as far humbler homes, and a shrewd-headed businessman whose company remains an international byword for excellence after more than two centuries.

Erasmus Darwin was right: Wedgwood exemplifies the broad combination of talents and skills which Australia today so sorely needs if it is to take advantage of its greatest and most neglected asset, our knowledge base.

If we are not to fall behind our region, Australia needs a new generation of managers who combine business acumen with technological mastery, creativity with understanding.

It is of little use our products being scientifically brilliant if they are not also superbly engineered, aesthetically pleasing, cleverly attuned to customers' wishes and intelligently marketed. The true value is often in the latter part of the chain.

Science, technology, design and information will be the determinants of business success in the coming decades. They will decide whether an individual or a company is admitted to the corridors of progress, or languishes sadly in the provincial hinterland.

Ladies and gentlemen, Australia is already so richly endowed with the potential to gain admittance to these corridors of the future, that it is a matter of wonder we have made so little progress.

In my introduction I emphasised that food, population and the environment will be the focal issue of the coming century. Is there any country in the world with richer credentials in the area of sustainable land and water management? Which grows a wider range of animals and plants in so many different environments? Which knows more about the unique system known as landcare, whereby whole communities come together to manage their catchments and districts more sustainably?

If the world faces a crisis over water, land and food, then Australia also has answers to that crisis. We have the knowhow to defuse disaster.

Our minerals industry has concentrated for years on the export of raw materials—but in the past five years there has been a quiet revolution. It has become a knowledge exporter. Last year sales of mining knowhow exceeded $500 million—more than nickel or diamonds. With strong growth in demand for green mining technology, for techniques like the Hi-smelt steelmaking process, the potential is there for knowledge exports to join coal and gold as one of our top three mineral exports.

In medicine, health and nutrition Australia has a superb scientific track record which is at last starting to be converted into commercial advantage through firms such as F. H. Faulding, CSL, AMRAD, Peptech, Biota and the like. However one of our greatest opportunities lies in the development of systems which *prevent* disease, instead of simply curing it. The CSIRO Division of Human Nutrition is leading research into foods which are carefully profiled to combat heart disease, cancer and other degenerative disorders. Worldwide, prosperous societies are seeking foods which are not only clean, safe and delicious—but also which preserve one's vigour, youthfulness and good health. Nowhere is demand for such foods stronger than among the rising middle classes of Asia—and this too must surely be one of our greatest opportunities.

I also described how humanity was now in collision with the earth's natural resources. In future we must all make more from less. We must recycle water safely, return nutrients to the land, use more renewable energy, and exploit what for many of us today is regarded as simply waste. Indeed, I venture to predict that our urban waste streams will become the mines of the future. But there are many other things which can also be harvested from the waste stream—metals and minerals, nutrients, fibre and energy, even fresh water.

Australia is a world leader in devising technologies to recycle and re-use wastes, to protect

and monitor natural systems. And companies like Pratt Industries are turning this knowledge to commercial advantage here and in the United States.

We urgently need to realise value from all this knowledge through a new breed of Australian — technologically savvy, commercially shrewd, and sensitive to issues such as aesthetics and the environment.

They must have the education and training which enables them to penetrate the corridors of progress and development. A science or engineering degree is no longer sufficient. It must be mated with other skills — law, commerce, Asian languages, communication, and the humanities and social sciences.

Today one of the greatest challenges facing us all is how to adapt technology for society, rather than the other way around. We desperately need young Australians who bridge both worlds, who combine both sets of skills, who can understand the technology but are also alive to the concerns and anxieties of ordinary people about how it will change their lives.

A clever country is not merely a scientific society. We are already that. A clever country is one which is adroit at adapting science to people. It is also a society capable of imagination — and swift, decisive action. A society of the intellect,

as well as one which makes wise use of natural resources.

What of Lucy's Choice? Lucy is my elder daughter and, having charted the choppy waters of the VCE assessment tasks and exams, she has embarked on one of the exciting bridging options, a law-science degree at Monash University. It was *her* career decision and that of her friends that led me to search my own experience for people who make a difference. They are always bridging people — Sir Gus Nossal, magnificent scientist and brilliant communicator, Dr Jose Herrero, a medical doctor who ran the licensing department at Hoffman la Roche in Basel — a consummate businessman, scientist and wit, Dr John White, the American patent attorney who skilfully guides the Gene Shears intellectual property through the USA Patent office using his deep awareness of the molecular biology and of the legal and procedural requirements, Richard Pratt who is the closest Australian I can find to Josiah Wedgwood, with whom we began this reverie ...

Ladies and gentlemen, I believe that our youngsters *are* awake to our nation's need. Lucy's choice confirms me in this. We must recognise the reality of the changed world and set our nation's policies to use best the skills, the intelligence, the creativity and the imagination which Australia will need to be the gold rush country of the 21st Century.

JOHN STOCKER FTS FRACP

Dr John Stocker was appointed Director, Research and Innovation, Pratt Industries in April 1995 on the completion of his five year term as Chief Executive of CSIRO Australia.

In 1970, Dr Stocker graduated top of his year in medicine at the University of Melbourne, and embarked on a career in Medical research. After his residency at the Royal Melbourne Hospital, he completed his Doctorate of Philosophy thesis at the Walter and Eliza Hall Institute of Medical Research in Melbourne under Sir Gustav Nossal.

From 1976 to 1978 Dr Stocker was a member of the Basel Institute for Immunology in Switzerland.

He joined the Swiss pharmaceutical company Hoffman-La Roche and Co. in its Basel headquarters in 1979. His first position in the company's Central Research Unit involved working on monoclonal antibodies and leading an international task force into the scientific and commercial opportunities offered by biotechnology-based vaccines.

In 1986, he was appointed the company's Director of Pharmaceutical Research and joined Hoffman-La Roche and Co's international Research Board.

Dr Stocker returned to Australia in 1987 to become the founding Managing Director of AMRAD Corporation Ltd, a company established to commercialise Australian biomedical discoveries.

He joined CSIRO in march 1990 as the first Chief Executive to be appointed from outside the Organisation.

Dr Stocker is a Director of Cambridge Antibody Technology Ltd, Circadian Technologies Ltd and Rothchild Bioscience Managers Ltd. He was a foundation member of the Prime Minister's Science Council, a member of the Australian Research Council and a member of the Australia China Council.

Dr Stocker is married and has two daughters. He plays tennis and has interests in viticulture and Australian native trees. The *Australian* newspaper named him 'Australian of the Year' in February 1992.

BOOK REVIEW

MOORE, K., 1995. *A Guide to the Archives and Manuscripts of the Royal Society*. The Royal Society, London, 73 pp. Price £15.00 (UK), £16.50 (overseas).

The Royal Society, London, founded in 1660 and granted its royal charter in 1662, is a prime example of the establishment of scientific societies established throughout Europe during the mid-seventeenth century. The purpose of the Royal Society was to investigate nature in the hope that this would result in English industry becoming more profitable, competitive and efficient (Burke 1985). The Royal Society was not hampered by the strict censorship that restricted kindred societies such as the Royal Academy of Sciences, Paris, where the theories of René Descartes were not allowed to be discussed.

It is scarcely surprising that the Royal Society in nearly 350 years of history has amassed, and is the guardian of, records and other archival material that provides fundamental insights into the development of science in Great Britain and, indeed, western scientific thought in general. However, for all the treasures contained within the archives to be of maximum use they must be catalogued and accessible. Hence it is with a considerable sense of welcome, that this volume by Keith Moore (Royal Society Archivist 1986–1990) with additions by Mary Sampson (Royal Society Archivist 1991–) has been published. The Royal Society did not have an archivist until 1950. As noted by Professor Alan Cowey FRS in the foreword to this *Guide*, the Archives of the Royal Society were scattered throughout the Society's old premises in Burlington House but with the move to Carlton House Terrace in 1967 an opportunity for consolidation presented itself.

The *Guide* consists of two main sections. Part one is a simple listing of the organisational cataloguing of the Archives and Manuscripts. Included are categories such as administrative records, administrative correspondence, scientific papers and correspondence, biographical records of Fellows, manuscript collections, collections of Fellows' personal papers (pre-20th Century), collections of Fellows' personal papers (20th Century), collections of artefacts and archives of other organisations. Part two, the bulk of the *Guide*, is a short description of the main series and it is here that we are able to obtain a glimpse of the wealth of material in the Archives.

The Journal Books contain the minutes of ordinary meetings from 1660. Prior to the 19th Century, letters and papers read before the Society are given in abstract and include any subsequent discussion. Minutes of the meetings of Council from 1663 include records of discussions on activities, awards, funds and bequests, buildings and staff. The Letter Book Original (1661–1740) provides copies of letters received by the Society. The Society holds the originals of the three charters granted by Charles II (1662, 1663 and 1669), incorporating the Society and authorising its rights and privileges.

The International Relations Archive includes correspondence and papers relating to the Royal Society's relations with the International Council of Scientific Unions (ICSU). Included within the Archive is material on the establishment of and scientific results from the Royal Society Base at Halley Bay, Antarctica.

Original manuscripts of Royal Society correspondence include the *Early Letters* (38 volumes containing 4237 items) including material by Henry Oldenburg, John Beale, John Flamsteed, Martin Lister, Isaac Newton, Antoni van Leeuwenhoek, Christiaan Huygens, J. D. Cassini and Cotton Mather. A series of unpublished, or only abstracted, papers from 1768–present are included within the Archives.

The largest and most diverse series of papers within the Archives are classified as *Manuscripts (General)* and includes collections of documents donated, purchased or otherwise acquired from outside sources. The range of this collection is large but includes administrative records, administrative correspondence, correspondence of Fellows and other scientists (including William Buckland, John Flamsteed, John Burden Sanderson Haldane, Marcello Malpighi, Joseph Priestly, Edward Sabine, James Sowerby and Walter White) and selected manuscripts and notebooks by Fellows such as the manuscript of *Philosophiae Naturalis Principia Mathematica . . .* by Isaac Newton (1642–1727).

Other significant archival collections include the correspondence of Robert Boyle (1627–1691) with seven volumes of letters, the Boyle Papers of forty-six volumes, the Herschel letters (in all 10 600 + letters of the correspondence of Sir John Frederick William Herschel FRS, 1792–1871, astronomer and secretary of the Royal Society 1824–1827) and the Smeaton Drawings (John Smeaton FRS, 1724–1792, civil engineer, the collection including working drawings for windmills, fire engines, bridges, buildings, canal works and harbours and river

navigations). Additional collections include the Bawden Papers (Sir Frederick Charles Bawden, 1908–1972, plant pathologist), the Blackett Papers (Patrick Maynard Stuart Blackett OM, Baron Blackett of Chelsea, 1897–1974, nuclear physicist), the Dale Papers (Sir Henry Hallett Dale GBE, OM, 1875–1968, physiologist–pharmacologist), the Jeans Papers (Sir James Hopwood Jeans OM, 1877–1946, mathematician, physicist and astronomer) and the Robinson Papers (Sir Robert Robinson OM, 1886–1975, chemist) to name but a few.

Probably the largest single collection of personal papers in the Society's care is the scientific and personal papers of Howard Walter Florey OM (Lord Florey of Adelaide, 1898–1968, experimental pathologist), consisting of 369 boxes or volumes of material, 100 books from Florey's library and 81 boxes of reprints and card files.

The Archival collections of the Royal Society also include museum objects and presentations, such as a valuable collection of chronometers including examples of the work of Thomas Tompion (1639–1713) and John Arnold (1736?–1799), medals, prints and portraits and busts.

The *Guide* concludes with the regulations governing the use of the library and archives, guidelines on access to the archives of the Royal Society, the Bibliography of works referred to in the text and an index of persons and institutions. The volume is logically presented in clear type and an added bonus are the illustrations which include a pen and ink drawing of Charles II, a sketch of Newton's apple tree in 1840, the Great Melbourne Telescope completed in 1867, sketches of Saturn by Christopher Wren and the portrait of Lord Howard Florey by Henry Carr.

Keith Moore and Mary Sampson are to be congratulated on their description of the Archives and Manuscripts of the Royal Society. The volume should be of great interest to scientists and technologists, particularly to those with an interest in the history and philosophy of science, and should find its way into many an individual's personal library as well as institutional libraries.

REFERENCE

BURKE, James, 1985. The Day the Universe Changed. British Broadcasting Corporation, London, 352pp.

N. W. Archbold
School of Aquatic Science and Natural Resources Management
Deakin University
Clayton, Victoria 3168, Australia

FISSION TRACK THERMOCHRONOLOGY OF SOUTHEASTERN AUSTRALIA: UNIQUE PERSPECTIVES ON THE EVOLUTION OF OUR CONTINENTAL MARGINS AND MOUNTAINS*

Andrew J. W. Gleadow

Victorian Institute of Earth and Planetary Sciences, School of Earth Sciences, La Trobe University, Bundoora, Victoria 3083

Gleadow, A. J. W., 1966:12:31. Fission track thermochronology of southeastern Australia: unique perspectives on the evolution of our continental margins and mountains. *Transactions of the Royal Society of Victoria* 108 (2): 9–15. ISSN 0035-921.

The accumulation of radiation damage from the spontaneous nuclear fission of ^{238}U is the basis of a thermally-sensitive geological dating technique which can be applied to common uranium-bearing minerals. Fission tracks in the mineral apatite are stable over geological time only at relatively low temperatures, below about 120°C, which are characteristic of the upper few kilometres of the Earth's crust. Fission track ages and track length distributions reflect the cooling history of rock masses that have passed through this upper-crustal domain. Broad regional patterns of fission track data are primarily controlled by large scale earth movements which initiate cooling in rocks through denudation at the Earth's surface. New interpretive techniques now enable these thermal and tectonic processes to be quantified and mapped out in considerable detail.

Studies in southeastern Australia using these methods reveal a striking imprint of tectonic activity related to continental breakup on the eastern and southern margins of Australia. A major element in the patterns is an overall decrease in fission track age towards the continental margins indicating higher palaeotemperatures and generally greater depths of erosion in this direction. In detail, however, the pattern is more complex than this and a number of regional variants are visible. In western Victoria there is an abrupt transition in behaviour which appears to terminate the breakup style characteristic of most of eastern Australia. Tasmania shows a generally deeper erosional level which may reflect its position within the evolving rift system during the separation of Australia and Antarctica.

THE accumulation of radiation damage from the spontaneous nuclear fission of ^{238}U is the basis of a geological dating technique which can be applied to a number of common uranium-bearing minerals, such as apatite and zircon. This simple method of geological dating was first described over thirty years ago (Price & Walker 1963) and has undergone a rapid development, particularly over the past fifteen years, both in terms of understanding the fundamental systems involved and in the diversity of its geological applications (see for example Wagner & van den Haute 1992).

Advances in defining the long-term stability of fission tracks at elevated temperatures and in modelling the response of the fission track dating system to changing temperatures have opened up what is now the major domain of application of fission track techniques — thermal history analysis, or thermochronology. Fission track thermochronology involves the using of fission track record in natural mineral systems to reconstruct the contrasting thermal histories which have occurred in various geological environments. The method is now applied across a wide range of geological studies, most significantly in analysing the thermal history of sedimentary basins, the tectonics of young mountain belts, and the evolution of rifted continental margins. The purpose of this paper is to briefly review the application of fission track thermochronology in southeastern Australia.

FISSION TRACK DATING

When a uranium nucleus contained in a natural mineral decays by spontaneous nuclear fission, the energy released is largely carried away as kinetic energy by the two fission fragments produced. These two highly energetic, and highly charged, particles fly apart from each other through the surrounding crystalline lattice and produce a single linear trail of radiation damage, known as a 'fission track'. The damaged region making up the fission track is highly chemically reactive compared to the surrounding undamaged material. As a result, fission tracks can be enlarged by a simple chemical etching procedure until they can be observed and measured by optical microscopy. The etching of fission tracks is illustrated diagrammatically in Fig. 1.

The number of tracks revealed in this way on a polished surface of a mineral grain will be proportional to the time over which tracks have been accumulating, and the amount of uranium present. A thermal neutron irradiation procedure is used to artificially induce a second set of fission tracks, the number of which is proportional to the uranium concentration. The ratio, then, of the number of spontaneous fission tracks to the number of induced tracks gives a measure of geological age.

FISSION TRACK ANNEALING AND MODELLING

An important aspect of fission track dating is that the radiation damage making up the tracks is stable over geological time only at relatively low temperatures. As temperatures increase, the radiation damage making up the tracks is repaired by a diffusional process known as fission track annealing. This does not occur suddenly but rather takes place progressively over a broad temperature interval called the fission track annealing zone. The effect of geological annealing is that the fission track age becomes gradually reset, eventually reaching zero above the critical temperature at which the tracks are completely erased. Such a reduction in the apparent fission track age is accompanied by a progressive shortening of the tracks which can be measured to monitor the degree of annealing that has occurred (Gleadow et al. 1986).

The lengths of fission tracks are all very similar when first produced so that the observed distribution of lengths after annealing contains a record of the variation in temperature that has occurred over the lifetime of the host mineral. The underlying kinetics of fission track annealing are now well understood, at least for some minerals, from quantitative laboratory annealing experiments (e.g. Laslett et al. 1987; Green et al. 1989) and a variety of geological studies in well controlled environments. The resulting annealing models enable a detailed reconstruction of the thermal histories of rocks from the observed patterns of fission track lengths and apparent ages (Gleadow 1990; Gallagher 1995).

Fission track annealing occurs over a different temperature interval for each of the minerals used for fission track dating. Fission tracks in the common calcium-phosphate mineral apatite, for example, are stable over geological time only at temperatures below about 120°C. Such temperatures are characteristic of the upper few kilometres of the Earth's crust so that apatite ages reflect the cooling history of rock masses as they pass through this upper-crustal domain. Usually these apparent ages display little relationship to the original formation ages of the rocks but often reflect large scale earth movements which initiate episodes of cooling through erosion at the Earth's surface.

Fig. 2 shows a hypothetical cooling history from 300°C down to an ambient surface temperature of 20°C over a time period of 360 Ma. The
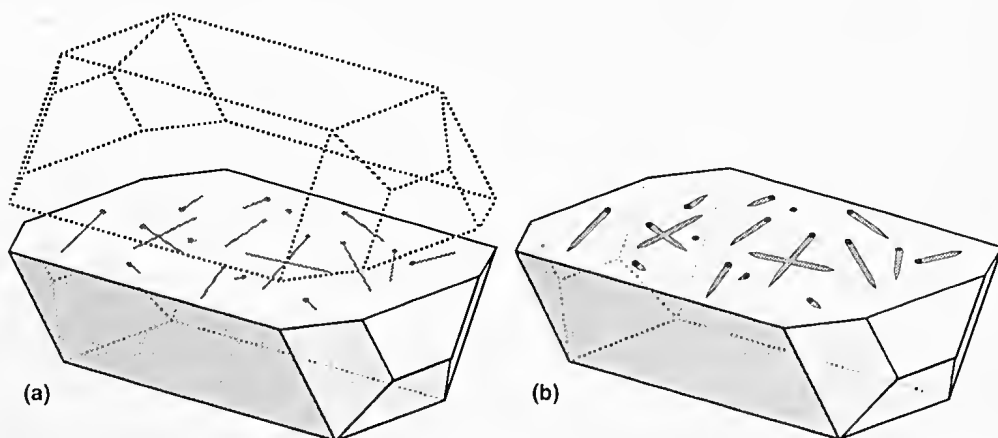

Fig. 1. Fission tracks are revealed in a crystal of a uranium-bearing mineral, such as apatite, by first cutting and polishing a smooth surface through the crystal (a). Fission tracks that cross this surface are then accessible to chemical etching which enlarges the tracks until they can be seen under an optical microscope (b). Fission tracks in apatite are etched in dilute nitric acid and have a needle-like shape. They measure about 16 μm in length and 1–2 μm across.

temperature-time path shows an initial rapid cooling, followed by very slow cooling between about 300 and 100 Ma and then rapid cooling again between 100 and 80 Ma. The diagram also shows calculated fission track ages and fission track length distributions for two minerals, apatite and zircon, calculated using the annealing model of Gallagher ct al. (1995). The fission track anncaling zone for zircon occurs at much higher temperatures and the shape of the track length distribution reflects the simple, rapid cooling of the host rock through this range. The zircon apparent age directly reflects the rapid cooling through the zircon annealing zone and may closely approximate the formation age of an igneous rock at even higher temperatures.

Cooling through the apatite annealing zone in Fig. 2 is more complex and the fission tracks recordcd by the apatites resolve into two distinct componcnts rcflected in thc bimodal length distribution. The shorter peak reflects those earlier formed tracks which pre-date the rapid cooling at about 100 Ma and have all been severely shortened by annealing at relatively high tcmperatures. The longer peak, in contrast reflects those tracks which have formed since about 80 Ma at relatively low

temperatures. The apatite apparent age in this case is a mixture of both these components of tracks and does not directly indicate the timing of any particular geological event. Such mixcd ages are relatively common and the interpretation of a suitc of apatite ages dcpends critically on an understanding of the associated track length data.

Using these modelling techniques it is possible to reconstruct thermal histories which match the fission track data in a particular sample. Applying this to many samples throughout a broad arca allows the overall pattern of regional cooling events to be established which can then be interprcted in terms of past tectonic and thermal activity, and patterns of surface denudation.

FISSION TRACK THERMOCHRONOLOGY IN SOUTHEASTERN AUSTRALIA

Studics in southeastern Australia over the past twenty years using these methods have revealed a striking imprint of tectonic activity relatcd to continental breakup on the eastern and southern margins of Australia (e.g. Moore et al. 1986; Dumitru et al. 1991; Foster & Gleadow 1992; Hill et al. 1995). The overall pattern of apatite
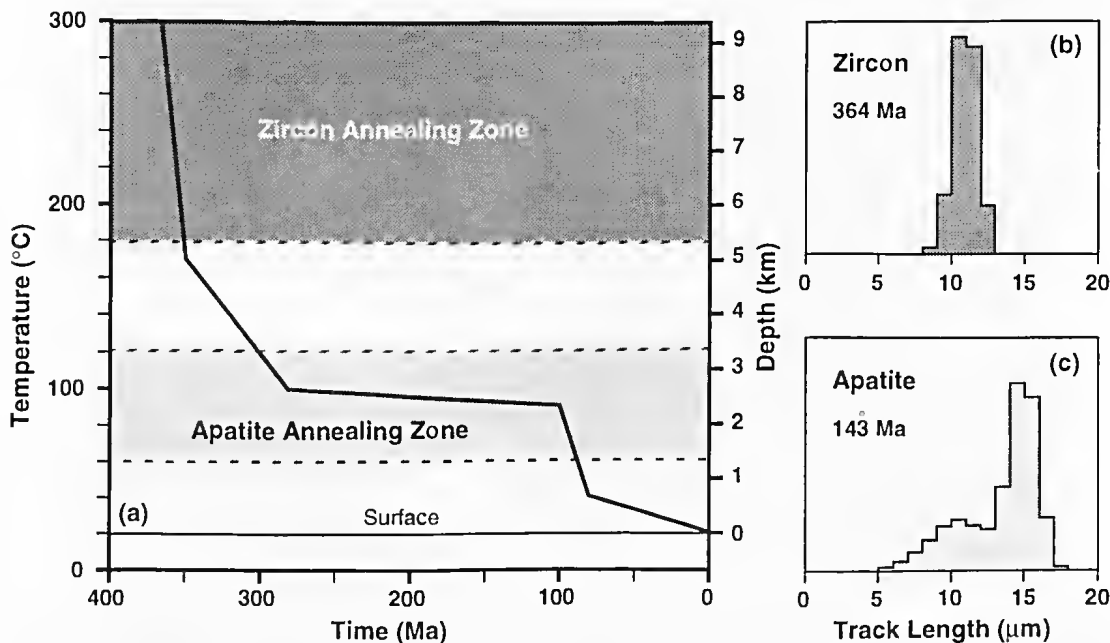

Fig. 2. A hypothetical thermal history for a rock showing a two-stage pattern of cooling from about 300°C over the last 360 million years (a). The diagram also shows the fission track annealing zones for the minerals zircon and apatite. The histograms (b) and (c) show the distributions of fission track lengths and apparent fission track ages for these two minerals calculated according to the modelling procedures of Gallagher (1995).

fission track ages in the Palaeozoic basement rocks of this region is shown in Fig. 3. The oldest apparent ages (up to 300 Ma or more) are associated with the inland regions of far-western Victoria or in the eastern highlands. Much younger apparent ages (down to 100 Ma or less) are found towards the continental margins. In general, the younger ages reflect later episodes of Mesozoic (mostly Cretaceous) cooling on a background of late Palaeozoic cooling ages. Intermediate apparent ages are frequently mixed ages as revealed by their distributions of track lengths (Moore et al. 1986).

The explanation for this pattern is that the eastern continental margin has been uplifted in a broad flexure towards the coast during the period of continental rifting leading up to the opening of the Tasman Sea by sea-floor spreading, about 80 million years ago (Moore et al. 1986). Erosion of the newly developed continental margin
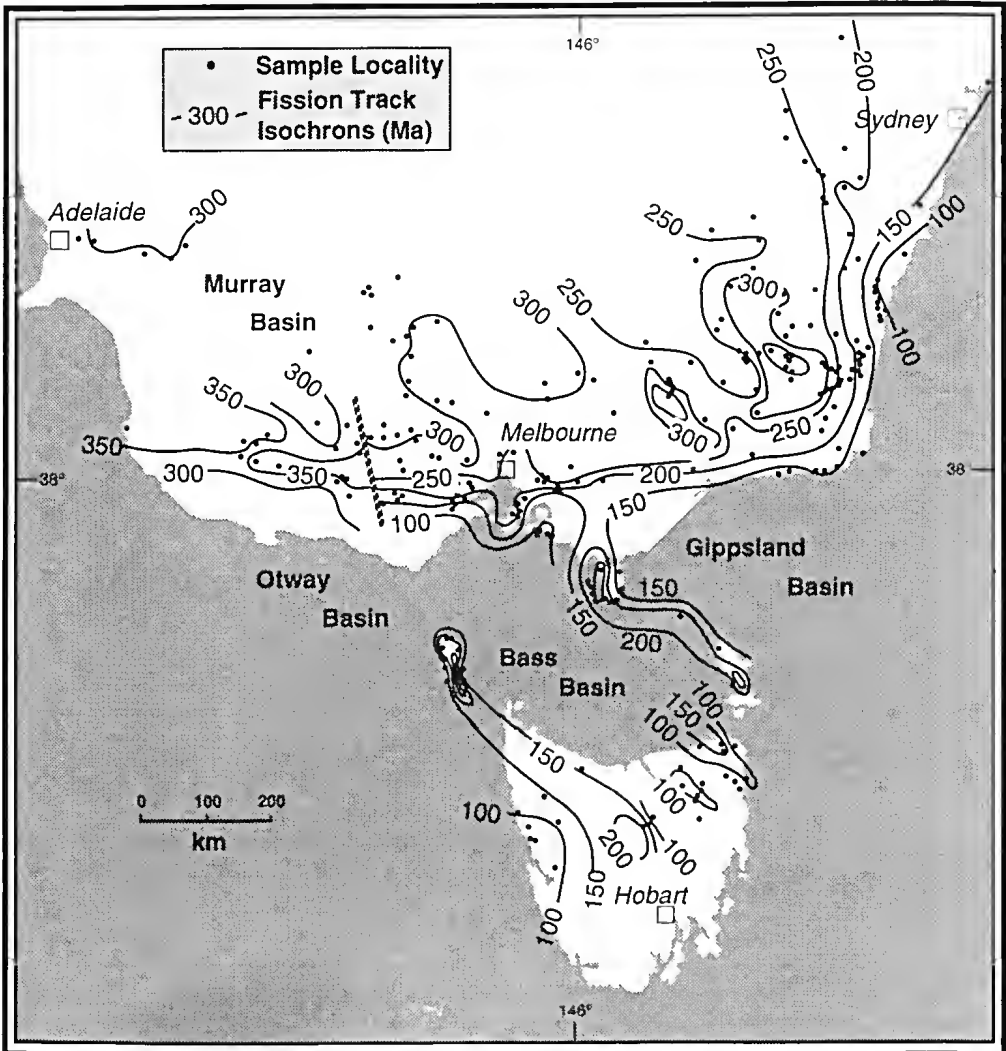

Fig. 3. The distribution of apparent fission track ages in apatites from Palaeozoic basement rocks around southeastern Australia (modified and updated after Moore et al. 1986 and Dumitru et al. 1991). The apparent ages show a broad regional variation from maximum values in excess of 300 Ma to minimum values of less than 100 Ma. On the mainland the youngest apparent ages invariably occur in a relatively narrow strip adjacent to the rifted continental margins and surrounding the Bass Strait Basins. In general, apatite ages from Tasmania are significantly younger than those on the mainland.

has allowed rocks near the coast to cool from temperatures that were previously within or above the apatite fission track annealing zone. The youngest apatite ages observed have been completely reset around this time and are broadly similar to the ages of the oldest adjacent oceanic crust as determined from sea-floor magnetic anomaly patterns (Weissel & Hayes 1977; Shaw 1978). Along the east coast the apatite ages near the coast show a tendency to become younger from south to north. O'Sullivan et al. (1995) have suggested that this may reflect the progressive opening of the Tasman Sea in that direction from about 80 to 60 million years ago.

The youngest ages are generally associated with long narrow length distributions characteristic of relatively rapid cooling. This indicates that in some coastal areas rocks now exposed at the surface were at temperatures of just over 100°C during continental breakup in Early to Middle Cretaceous time. Assuming a typical geothermal gradient of 25–30°C, this implies that erosion of up to 3–4 km has occurred in some areas since that time. The possibility that higher thermal gradients may have existed at this time allows the amount of denudation inferred to be reduced but probably to no less than about half these figures.

Similar patterns are observed around the margins of the major sedimentary basins in Bass Strait which were also formed during the main phase of continental rifting in the Cretaceous. The youngest apparent ages exposed in Palaeozoic rocks of southern central Victoria and in the older sediments of the Otway Basin are similar to those along the east coast. These younger ages broadly correspond to cooling during the development of the basins and may be associated with an early, limited phase of slow sea-floor spreading in the Southern Ocean during mid-Cretaceous time (Cande & Mutter 1982). The much later onset of rapid sea-floor spreading between Australia and Antarctica at about 45 Ma appears to have left no discernible imprint on the pattern of fission track ages.

TASMANIA

Tasmania (Fig. 3) shows generally much younger apatite ages than those observed on the mainland, even though in most cases these are also obtained from rocks formed during the Palaeozoic (Hill et al. 1995). This suggests that generally deeper erosional levels are exposed in Tasmania which may reflect its central position within the evolving rift complex during the continental breakup phase. The Island was completely surrounded by developing rift systems in the Cretaceous during the early phases of separation between the three large continental blocks of Australia, Antarctica, and the Lord Howe Rise/New Zealand. It is possible that the continental margin effects observed on the mainland may therefore have had an additive influence in Tasmania.

Another factor which is unique to Tasmania is the development of the very large and extensive
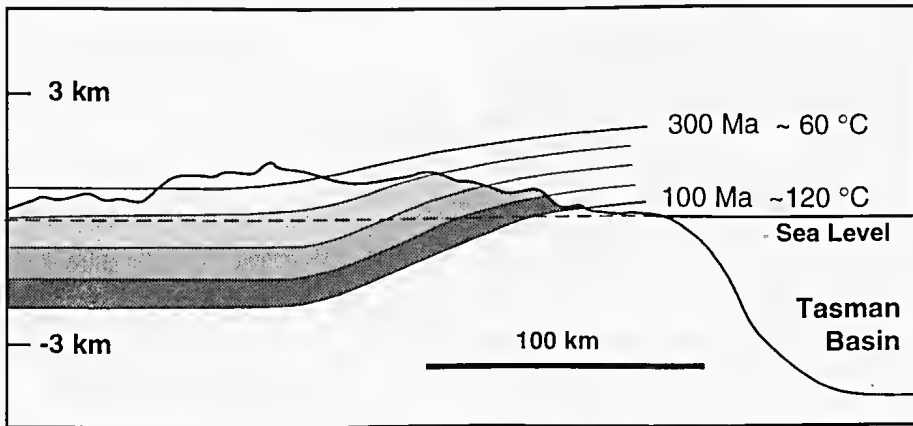

Fig. 4. A diagrammatic cross-section of southeastern Australia across the highlands to the continental margin in southern NSW. The shaded contours shows zones of decreasing apparent fission track age in apatites and how these are thought to be tilted upwards towards the coast in a broad flexure of the crust. The contours may also be taken to represent increasing palaeotemperatures in the crust during the Cretaceous (after Dumitru et al. 1991).

dolerite sills there during the Jurassic. These would have had the effect of raising temperatures across virtually the whole island to the point where it would be unlikely that fission tracks would survive in apatite. In this situation the entire pattern of apatite ages must post-date the Jurassic and are therefore starting from a much lower maximum than observed on the mainland. A similar ceiling effect caused by widespread Jurassic igneous activity has been observed in northern Victoria Land in Antarctica by Fitzgerald & Gleadow (1988).

WESTERN VICTORIA

In western Victoria there is an abrupt transition in behaviour which appears to terminate the structural style characteristic of the continental margin of most of eastern Australia. This can be seen as a marked change in the pattern of apatite fission track ages as shown in Fig. 3. West of this transition a completely different structure of the continental margin is apparent with no evidence for the broad crustal flexure found everywhere to the east (Foster & Gleadow 1992, 1993). This pattern is associated with extremely subdued topography which is typical of most of the southern margin of Australia and quite unlike the rugged eastern highlands which parallel the rifted margin to the east.

The transition in crustal architecture in western Victoria displays many of the characteristics predicted for an upper plate–lower plate boundary in the large-scale detachment model of Lister et al. (1991). Under this model the development of a continental margin is dominated by the formation of a major low-angle normal fault, or detachment, cutting obliquely through the continental lithosphere. One side of the developing rift, the lower plate, is then drawn out from beneath the other upper plate in an extensional style that is markedly asymmetrical. This model is significantly different from earlier models in that it predicts that the structure of the two separating plates will be different and that the polarity of the asymmetry may change periodically along the length of a rifted margin.

The transition in fission track pattern across western Victoria is relatively sharp and appears to follow a much older, Early Palaeozoic, boundary between the Delamerian and Lachlan Fold Belts. It is thought that this old crustal scale weakness may have been reactivated during Mesozoic rifting. The existence of this inherited weakness in the continental crust may also have played a fundamental role in locating the major transform plate boundary along the west coast of Tasmania which then transferred extension to the south of Tasmania during continental rifting. As a result the island remained as part of Australia, rather than Antarctica, despite the early phase of rifting through Bass Strait. The transform boundary is preserved today as the Tasman Fracture Zone which traverses the Southern Ocean to northern Victoria Land in Antarctica which was formerly adjacent to western Victoria prior to continental breakup.

SNOWY MOUNTAINS

The Snowy Mountains reveal a later modification of the regional architecture of the eastern continental margin with a structure dominated by large fault blocks elevated to varying degrees above the surrounding region, a structure still reflected in the present landscape (Cox et al. 1994). Overall uplift of the mountains is greatest on their western side, near Mt Kosciusko, and gradually steps down to the east (Kohn et al. 1994). Apatite ages of approximately 90 million years on the western side of the mountains probably date the onset of renewed tectonic activity in the eastern highlands generally, following a long period of quiescence during the late Palaeozoic and early Mesozoic. However, much of the present day relief of the mountains in this area is probably related to later, Tertiary, movements which have occurred along reactivated Palaeozoic faults. The uplift may be a response to the change in the crustal stress regime in this area from extension to the mild compression which now characterises southeastern Australia.

CONCLUSIONS

Fission track studies on the evolution of southeastern Australia have added considerably to our understanding the structural and geomorphic response of continents to extensional tectonic processes which occurred during the breakup of the former supercontinent of Gondwana. They have also made the area a major reference point for similar work being undertaken on rifted continental margin environments elsewhere in the world.

ACKNOWLEDGEMENTS

REFERENCES

Cox, S. J. D., Kohn, B. P. & Gleadow, A. J. W., 1994. Towards a fission track image of Australia: model based interpretation in the Snowy Mountains using a GIS. *Geological Society of Australia Abstracts* 37: 72–73.

Dumitru, T. A., Hill, K. C., Coyle, D. A., Duddy, I. R., Foster, D. A., Gleadow, A. J. W., Green, P. F., Laslett, G. M., Kohn, B. P. & O'Sullivan, A. B., 1991. Fission track thermochronology: application to continental rifting of southeastern Australia. *APEA Journal* 31: 131–142.

Fitzgerald, P. F. & Gleadow, A. J. W., 1988. Fission track geochronology, tectonics and structure of the Transantarctic Mountains in northern Victoria Land, Antarctica. *Isotope Geoscience* 73: 169–198.

Foster, D. A. & Gleadow, A. J. W., 1992. Reactivated tectonic boundaries and implications for the reconstruction of southeastern Australia and northern Victoria Land, Antarctica. *Geology* 20: 267–270.

Foster, D. A. & Gleadow, A. J. W., 1993. The architecture of Gondwana rifting in southeastern Australia: evidence from apatite fission track thermochronology. In *Gondwana 8—Assembly, Evolution and Dispersal*, Findlay, R., Unrug, R., Banks, R. H. & Veevers, J. J., eds, Balkema, Rotterdam, 597–603.

Gleadow, A. J. W., 1990. Fission track thermochronology—reconstructing the thermal and tectonic evolution of the crust. *Proceedings of the Pacific Rim Congress 1990*, Gold Coast, Queensland, 6–12 May 1990, Vol. III, 15–21.

Gleadow, A. J. W., Duddy, I. R., Green, P. F. & Lovering, J. F., 1986. Confined fission track lengths in apatite—a diagnostic tool for thermal history analysis. *Contributions to Mineralogy and Petrology* 94: 405–415.

Green, P. F., Duddy, I. R., Laslett, G. M., Hegarty, K. A., Gleadow, A. J. W. & Lovering, J. F., 1989. Thermal annealing of fission tracks in apatite: 4—Quantitative modelling techniques and extension to geological timescales. *Isotope Geoscience* 79: 155–182.

Hill, K. C., Hill, K. A., Cooper, G. C., O'Sullivan, A. J., O'Sullivan, P. B. & Richardson, M. J., 1995. Inversion around the Bass Strait Basins, SE Australia. In *Basin Inversion*, Buchannan, J. G. & Buchannan, P. G., eds, Geol. Soc. Lond. Special Publication 88: 525–547.

Kohn, B. P., Gleadow, A. J. W. & Cox, S. J., 1994. The rise of the Snowy Mountains—when and how much: evidence from apatite fission track thermochronology. *Geological Society of Australia Abstracts* 37: 226.

Laslett, G. M., Green, P. F., Duddy, I. R. & Gleadow, A. J. W., 1987. Thermal annealing of fission tracks in apatite: 2—A quantitative analysis. *Isotope Geoscience* 65: 1–13.

Lister, G. S., Etheridge, M. A. & Symmonds, P. A., 1991. Detachment models for the formation of passive continental margins. *Tectonics* 10: 1038–1064.

Moore, M. E., Gleadow, A. J. W. & Lovering, J. F., 1986. Thermal evolution of rifted continental margins: new evidence from fission track dating of apatites from southeastern Australia. *Earth and Planetary Science Letters* 78: 255–270.

Cande, S. C. & Mutter, J. C., 1982. A revised identification of the oldest sea-floor spreading anomalies between Australian and Antarctica. *Earth and Planetary Science Letters* 58: 151–160.

O'Sullivan, P. B., Foster, D. A., Kohn, B. P., Gleadow, A. J. W. & Raza, A., 1995. Constraints on the dynamics of rifting and denudation on the eastern margin of Australia: fission track evidence for two discrete causes of rock cooling. In *Proceedings of the 1995 PACRIM Congress*, Mauk, J. L. & St George, J. D., eds, 441–445.

Price, P. B. & Walker, R. M., 1963. Fossil tracks of charged particles in mica and the age of minerals. *Journal of Geophysical Research* 68: 4847–4862.

Shaw, R. D. 1978. Seafloor spreading in the Tasman Sea. *Australian Society of Exploration Geophysicists Bulletin* 9: 75–81.

Wagner, G. A. & Van den Haute, P., 1992. *Fission Track Dating*. Kluwer Academic Publishers, 285 pp.

Weissel, J. K., & Hayes, D. E., 1977. Evolution of the Tasman Sea reappraised. *Earth and Planetary Science Letters* 36: 77–84.

ASTHMA: AN INCREASING PROBLEM AND A CHALLENGE IN MANAGEMENT

The Symposium was held on the afternoon and evening of 21 August 1996 in the hall of the Royal Society of Victoria, 9 Victoria Street, Melbourne 3000

CONTENTS *page*

PREFACE

Asthma has everything. It is a problem of the affluent North rather than the impoverished South; and increasing study reveals it to be a many-faceted problem:

- The incidence of asthma is increasing.
- Susceptibility may have a genetic basis.
- Sensitisation in infancy appears to be environmentally influenced.
- The crucial environmental factors appear to be those of the domestic micro-climate.
- Life-threatening attacks can be triggered at any age.
- Triggers are many, both natural and man-made, and they are not necessarily related to the original cause of sensitivity.
- Knowledge and planning, enabling a timely response to severe attacks, makes many asthma deaths preventable.

More than may be so for most other medical conditions, asthmatics respond to informed and comprehensive management. In the case of asthma, there is a prize to be won.

The Royal Society, in conjunction with the National Asthma Campaign, held an afternoon/evening symposium at the Society's hall on this important topic. The speakers were three medicos and a botanist, and summaries provided by them are included below.

The National Asthma Campaign (NAC) began with a pilot media communication program in 1988 which brought together the major organisations in asthma including the business community. This initial venture led to the launch of the NAC in 1990. It consolidated the shared initiative of the Thoracic Society of Australia and New Zealand, The Royal Australian College of General Practitioners, the Pharmaceutical Society of Australia and the Asthma Foundation and was supported by the pharmaceutical industry.

The goals of the NAC are:

- to achieve correct diagnosis of most people with asthma;
- to bring about a decline in preventable deaths from asthma;
- to establish team management of asthma by patient, doctor and pharmacist, so that most people with asthma will be following an individual action plan, developed with their doctor and assisted by their pharmacist.

MICHAEL ABRAMSON

CAUSES AND TRIGGERS OF ASTHMA

It is not as simple to distinguish between the causes and triggers of asthma as might be expected. As a respiratory physician who only treats adults, I normally see asthmatic patients many years after the initiating events. For this presentation, I propose to discuss *causes*, by which I mean the genetic susceptibility and exposures which usually occur in early childhood, that lead to the development of asthma in the first place. I will then proceed to discuss *trigger factors* which can provoke an attack of asthma in someone who already has the condition. To complicate matters, some exposures are capable of acting both as causes and triggers.

Causes of asthma

A helpful model of the development of asthma is summarised in Fig. 1. Asthma comprises at least two underlying traits: allergy and bronchial hyperreactivity. Allergy is the tendency to produce excessive amounts of a particular type of antibody (IgE) in response to otherwise innocuous foreign proteins (allergens) in the environment. Bronchial hyperreactivity (BHR) is the tendency of the airways to narrow excessively in response to allergens or other nonspecific stimuli. Allergy and BHR are seen in most (but not all) patients with asthma.

Asthma genes. There is no doubt that asthma runs in families and some of the genes responsible for this have recently been discovered. Researchers in Oxford have identified mutations in one of the IgE receptor genes on the long arm of chromosome 11, which they claim are associated with allergies. Other groups have been unable to confirm these observations. We have found linkage between this location on chromosome 11 and BHR, rather than allergies (Van Herwerden et al. 1995). This suggests that other genes on chromosome 11 may be responsible for the susceptibility to asthma and the search for these genes is already underway.
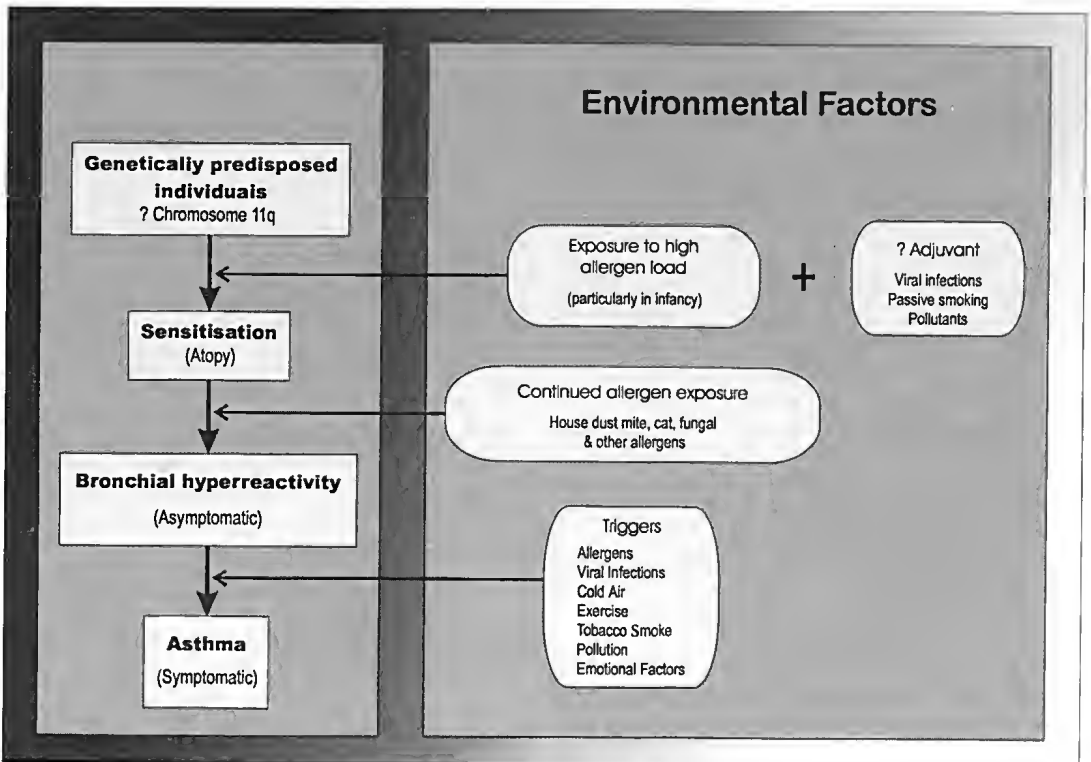

Fig. 1. Hypothesised progression from allergy to BHR to asthma.

There has also been considerable interest in a cluster of genes on the long arm of chromosome 5. Researchers at Johns Hopkins have found evidence for inheritance of high IgE levels in the Amish linked to a location near one particular gene (Interleukin 4) on this chromosome. Researchers at Southampton have found linkage between IgE levels and another gene (Interleukin 9) in this region. Furthermore, an American–Dutch collaboration has linked a nearby location to BHR in asthmatic families from the Netherlands. These exciting developments in the genetics of asthma have been well reviewed elsewhere (Wilkinson et al. 1996).

Childhood exposures. One of the complexities of asthma is that it arises from an interaction between the genes and environmental exposures, mostly occuring in infancy and early childhood. The developing immune systems of young children are bombarded with a wide variety of allergens in Western societies. These include the fine faecal particles of house dust mites, which are inevitable inhabitants of our bedding and carpets. New Zealand researchers have recently found astronomical levels of dust mite allergens in babies' sheepskin bedding. There is good evidence from Southampton that exposure to high levels of dust mites during the first month of life substantially increases the risk of developing dust mite allergy and asthma later in childhood (Warner & Warner 1996).

Pet ownership is common in Australia. Cat allergens are like the smile of the Cheshire cat; they hang around indoors for a long time after the cat has disappeared. Again the Southampton group has found that exposure to cats during the first month of life substantially increases the risk of developing cat allergy and asthma later in childhood. Contrary to popular belief, we now know that milk does *not* make mucus. However there is considerable interest in the role of dietary factors in the development of asthma. Children are now exposed to a wide variety of food additives from an early age. Recently it has been suggested that regular intake of oily fish may lessen the risk of asthma.

Occupational exposures. Although it commonly starts in childhood, asthma can begin at any age. Occupational asthma is a good example of the progression from susceptibility to allergy to BHR and symptoms. The causes can be classified as animal, vegetable, microbial or mineral (Newman-Taylor 1988). Susceptible laboratory workers who handle furry animals develop allergies and asthma in much the same way as children exposed to dust mite or cat allergens. A slightly different process occurs in carpenters exposed to western red cedar sawdust. In this situation, a small molecule needs to bind tissue proteins to set off an allergic reaction, which eventually results in asthma.

There are many other high risk occupations, such as aluminium smelting where occupational asthma has been recognised as a problem for 60 years, but the cause has not yet been identified. One of the key features of occupational asthma is the window of vulnerability. It is during the first few weeks of exposure in a new job that most cases of sensitisation arise. Another important concept is the minimum exposure dose and considerable effort has gone into defining safe exposure limits. Very high exposures to irritant gases such as sulphur dioxide or chlorine will result in a condition similar to occupational asthma, even in workers with no predisposing features.

Triggers of asthma

Some of the causes of asthma can also act as triggers for attacks, once the condition is established. This is certainly the case for house dust mite and cat allergens. On the other hand, air pollution doesn't cause asthma, but can probably trigger attacks. Many asthmatic patients are affected by a wide range of nonspecific irritants including cigarette smoke, perfume, hairspray and household bleach. Viral infections and exercise are common triggers for asthma attacks, particularly in children. The role of dietary factors is controversial.

Allergens. Once sensitisation has occurred, further exposure to allergens will trigger attacks of asthma. Thus we advise our dust mite allergic patients to avoid dusting or vacuuming. It was thought that exposure needed to exceed a threshold level of house dust mite allergen to produce symptoms, but there is now evidence of a dose response relationship at lower levels of exposure. The cartoon book *One hundred and one uses for a dead cat* was written by an asthmatic with severe cat allergy. Pollen allergic asthmatics are prone to dramatic seasonal attacks, which will be further discussed by Professor Knox.

I would like to share with you some fairly recent work on mould allergy. Researchers from the University of Sydney demonstrated that allergy to the mould *Alternaria* is the strongest risk factor for asthma among children in Wagga Wagga.

The strongest risk factor for asthma among young adults in Melbourne now appears to be allergy to the mould *Cladosporium*, the black mould many of you probably have growing in your bathrooms (Abramson et al. 1996). We have found higher levels of *Cladosporium* spores in the home of asthmatics and in the home of those with *Cladosporium* allergy than in the homes of nonallergic controls.

Air pollution.   It is a popular misconception that the rising prevalence of asthma must be due to air pollution. In fact the prevalence of asthma is much lower in eastern Germany than in western Germany, whilst air pollution was unquestionably much worse in the east. However I wouldn't want you to conclude that air pollution has nothing to do with asthma. There have been some intriguing experiments suggesting that pre-exposure to ozone or nitrogen dioxide increases the response of the airways to allergens such as house dust mite or grass pollen (see Abramson et al. 1995). Both these gases are major constituents of photochemical smog, which certainly occurs in Sydney and Melbourne, although not to the same extent as in Los Angeles.

In Western societies, indoor air pollution probably results in more potential adverse health effects than outdoor air pollution. Nitrogen dioxide is also given off by unvented gas appliances and can accumulate in quite high concentrations indoors. A recent study in East Anglia found that gas cooking was associated with respiratory symptoms and impaired lung function in women, but not men (Jarvis et al. 1996). Other indoor pollutants which probably trigger asthma include woodsmoke and formaldehyde, which is released by foam insulation in mobile homes.

Cigarette smoking.   There was an epidemic of cigarette smoking after World War II, which has only recently been brought under control. Active cigarette smoking was finally proved to cause lung cancer by the US Surgeon General in 1964 and chronic bronchitis and emphysema not long after. There is now a scientific consensus that passive smoking has deleterious effects in asthma (see Abramson et al. 1995). Furthermore, environmental tobacco smoke may act as a cofactor with allergens in the development of allergies in children. These were among the pieces of evidence cited by Justice Morling in his landmark ruling, which has seen smoking banished from most workplaces.

Viral infections.   The most frequent triggers of asthma attacks are upper respiratory tract infections (or colds). New highly sensitive techniques have shown evidence of viral infections in over 80% of wheezing illnesses in children (see Abramson et al. 1995). Conversely wheezing has occurred in 50% of respiratory viral infections in asthmatics followed prospectively. Although many studies have suggested an association between early respiratory illness and asthma, it is not at all certain that this is the cause and effect. Indeed there is some evidence that early respiratory infections may protect against the subsequent development of allergies.

Dietary factors.   Many patients with asthma report that particular foods worsen their condition. However these reports are notoriously difficult to confirm with placebo controlled double blinded food challenges. The parents of asthmatic children frequently attempt dietary modification, with little objective evidence of benefit. There are well documented reports of asthma attacks following the ingestion of food additives such as tartrazine and metabisulphite. Monosodium glutamate (MSG) which is used as a flavour enhancer in Chinese food, has received bad press as a trigger for asthma, but does not seem to have much effect on lung function tests performed in our laboratory. On the other hand, so-called 'natural' products such as Royal Jelly can cause life threatening allergic reactions in asthmatics.

Exercise.   Exercise particularly in cold dry air is a potent trigger of asthma attacks. This is the reason that many asthmatic children have been encouraged to take swimming lessons. Warm moist air is much less likely to trigger attacks. It is thought that cold air dries out the lining of the airways causing the release of chemicals such as histamine, which make the muscles surrounding the airways contract and bring about an attack of asthma. These attacks can be effectively prevented by premedication.

Prospects for prevention of asthma

To prevent asthma developing in the first place will require much more knowledge of the underlying causes. The recent advances in genetics will hopefully allow us to more accurately identify infants at a high risk of developing the condition. The environmental modifications required are likely to include a major redesign of Western style housing. Occupational asthma can be prevented by substitution of safer chemicals and control of

workplace exposures. The prevention of attacks in people who already have asthma will be discussed by Dr Pierce.

References

ABRAMSON, M., MARKS, G. B. & PATTEMORE, P. K., 1995. Are nonallergic environmental factors important in asthma? *Medical Journal of Australia* 163: 542–545.

ABRAMSON, M., KUTIN, J. J., RAVEN, J., LANIGAN, A., CZARNY, D. & WALTERS, E. H., submitted for publication 1996. Risk factors for asthma among young adults in Melbourne, Australia.

JARVIS, D., CHINN, S., LUCZYNSKA, C. & BURNEY, P., 1966. Association of respiratory symptoms and lung function in young adults with use of domestic gas appliances. *Lancet* 347: 426–431.

NEWMAN-TAYLOR, A., 1988. Occupational asthma. *Postgraduate Medical Journal* (Suppl. 4): 41–47.

VAN HERWERDEN, L., HARRAP, S. B., WONG, Z. Y. H. et al., 1995. Bronchial hyperreactivity rather than atopy is linked to the high affinity IgE receptor gene on chromosome 11q13. *Lancet* 346: 1262–1265.

WARNER, J. O. & WARNER, J. A., 1996. Early life origins of asthma and related allergic disorders. *Curriculum of Allergy to Clinical Immunology* 9(1): 10–16.

WILKINSON, J., HOLGATE, S. T. & THOMAS, S., 1996. The genetics of asthma and atopy. *Curriculum of Allergy to Clinical Immunology* 9(1): 3–10.

DON CAMPBELL

WHO GETS ASTHMA?
WHO DIES FROM IT?

Summary

The prevalence of asthma in Australia has risen in recent years. The prevalence of current asthma in South Australia rose from 5.6% to 9.0% between 1987 and 1990. In 1994 the cumulative prevalence of asthma in the Australian population was 15.3%. Studies of asthma prevalence in 8- to 11-year-olds conducted in the same community demonstrate a rise in prevalence of current asthma from 6.5% to 9.9% between 1982 and 1992, and a rise in the cumulative prevalence of diagnosed asthma from 12.9% to 19.3%.

Genetic factors are important in the development of asthma and atopy, however environmental factors appear to be crucial to the onset and persistence of asthma. These factors include changes in the indoor levels of house dust mite, levels of oxides of nitrogen and possibly diet (oily fish intake). Up to two-thirds of asthmatic children

continue to suffer from asthma through puberty and into adult life. Five to 10% of children with mild asthma are likely to develop severe asthma in later life. Children with moderate to severe asthma are at risk of long-term effects of asthma throughout life.

The age-adjusted asthma mortality rate in Australia increased from 2.7/100 000 in 1971 to 4.85 in 1989, declining to 3.53 in 1992. Between 1981 and 1992, for the very young ($<$15 years) the mortality rate was very low ($<$1/100 000) with little evidence of a change. For intermediate age ranges there was evidence of an initial rise and a subsequent reduction in mortality rates, whilst in the elderly mortality rates from asthma continue to rise. The positive predictive value of death certification due to asthma is very accurate in the under 55 age group, whilst in the over 64 age group the death certificate is not current enough to be used for epidemiological purposes.

Causative factors to explain the rise in mortality due to asthma may include the increased size of the at-risk population (prevalence), or a change in the severity of asthma. Detailed analyses indicate a large burden of preventable mortality due to asthma which reflects poor management including failure to recognise the severity of asthma, failure to manage asthma appropriately and poor compliance with asthma management plans.

Definition

'Asthma is a chronic inflammatory disorder of the airways in which many cells play a role. In susceptible individuals this inflammation causes symptoms which are usually associated with widespread but variable airflow obstruction that is often reversible either spontaneously or with treatment. It also causes an associated increase in airway responsiveness to a variety of stimuli.'

From the international consensus report on diagnosis and treatment of asthma, 1992.

1. Prevalance of asthma

The prevalence of asthma in Australia has risen in recent years. The prevalence of current asthma in South Australia rose from 5.6% to 9.0% between 1987 and 1990. In 1992 the prevalence of current asthma in Victorian adults was shown to be 7%. In 1994 the cumulative prevalence of asthma in the Australian adult population was 15.3%.

Studies of asthma prevalence in 8- to 11-year-olds repeated in the same community demonstrate a rise in prevalence of current asthma from 6.5% to 9.9% between 1982 and 1992, and a rise in the cumulative prevalence of diagnosed asthma from 12.9% to 19.3%. In a study of the prevalence of respiratory symptoms in South Australian pre-school children in 1993 the cumulative prevalence of asthma was 22.5%. This figure compares with the estimated prevalence of 17.1% in primary school age children across Sydney, Melbourne, Brisbane and the Upper Hunter Valley from 1992.

II.   Factors associated with the acquisition of asthma

Genetic factors are important in the development of asthma and atopy, however environmental factors appear to be crucial to the onset and persistence of asthma.

Up to two-thirds of asthmatic children continue to suffer from asthma through puberty and into adult life. Five to 10% of children with mild asthma are likely to develop severe asthma in later life. Children with moderate to severe asthma are at risk of long-term effects of asthma throughout life.

In 1968 a survey of all 7-year-olds in Tasmania was conducted, 85 855 children born in 1961 were surveyed, being 99% of the population. The cumulative prevalence of asthma was 19.0%.

A history of asthma was significantly associated with:

(i) the child being male (OR 1.56);
(ii) having an atopic background (OR 3.86 for hay fever);
(iii) having a family history of asthma (OR 2.63) this effect being additive on a log scale;
(iv) mother being a smoker (OR 1.26).

The familial aggregation of asthma is consistent with a genetic etiology, but also a shared environment.

As part of the study of the prevalence of respiratory symptoms in South Australian pre-school children, the relationship between prevalence of respiratory symptoms and indoor air quality was examined. Using a logarithmic regression analysis, the following factors were significantly associated with increased risk of asthma:

(i) natural gas stove compared with an electric stove (OR 1.24);
(ii) the use of a non-flued gas heater compared with other heating (OR 1.26).

Parental smoking was significantly associated with increased prevalence rates for bronchitis and ever having wheezed (OR 1.21 and 1.24).

Socio-economic status was not associated with prevalence rates for asthma.

Studies to examine the effect of environmental exposure upon the expression of asthma in children have included:

(i) the study of the effect of allergic sensitisation and climate upon the expression of asthma in children aged 8 to 11 years in seven climatic regions in New South Wales. In all regions the prevalence of current asthma was high (24 to 30%). The prevalence of current asthma was higher in 3 coastal regions where sensitisation to house dust mites was high, and in the far west of the state where sensitisation to *Alternaria* was high, compared with the prevalence in three inland regions where the sensitisation to these allergens was lower;
(ii) a study of school aged children in Sydney where sensitisation to house dust mite was shown to be a particularly important risk factor for both airway hyperreactivity and current asthma in Sydney schoolchildren. Children with large skin test reactions to house dust mite allergen were shown to be the group at greatest risk for morbidity affecting lifestyle.

The author suggests that measures to reduce the level of house dust mite in indoor air quality may have an effect upon the rate of sensitisation to house dust mite and of development of asthma.

In an interesting study of asthma and atopy in South-East Asian immigrants in Melbourne, Leung et al. (1994) found that Asian immigrants and Australian born Asians had a higher rate of atopy than in Australians, and that Asians were twice as likely to react to pollens than Australians and 1.5 times as likely to react to dust mite. Pollen reactors had a 4.8-fold increase risk for development of hay fever, and house dust mite monoreactors a 4.5-fold risk of wheeze or asthma. The prevalence of hay fever in Asian immigrants increased significantly with duration of stay in Australia, a lesser association was seen in duration of stay in Australia for asthma.

III.   The epidemiology of asthma mortality in Australia

The age adjusted asthma mortality rate in Australia increased from 2.7/100 000 in 1971 to 4.85 in 1989, declining to 3.43 in 1992. Between 1981 and 1992, for the very young (< 15 years) the mortality rate was very low (< 1/100 000) with little evidence of a change. For intermediate age ranges there

was evidence of an initial rise and a subsequent reduction in mortality rates, whilst in the elderly mortality rates from asthma continue to rise.

The positive predictive value of death certification due to asthma is very accurate in the under 55 age group, whilst in the over 64 years age group the death certificate is not accurate enough to be used for epidemiological purposes.

Where death certificates mentioned asthma but did not code the death as being due to asthma there was an excess of deaths attributable to diseases of the circulatory system and respiratory system, in the latter category chiefly due to chronic obstructive airways disease.

Thus Australian data points to the difficulty of distinguishing between asthma and other causes of chronic obstructive airways disease as potential causes of death in the older age groups.

IV. *What are the features of asthmatics dying of asthma?*

Causative factors to explain the rise in mortality due to asthma may include the increased size of the at-risk population (prevalence), or a change in the severity of asthma. Detailed analyses indicate a large burden of preventable mortality due to asthma which reflects poor management including failure to recognise the severity of asthma, failure to manage asthma appropriately and poor compliance with asthma management plans.

A principal objective of the South Australian Asthma Mortality Study was to test whether cases dying of asthma and asthmatics experiencing near fatal attacks (NFAs) were similar with regard to: their personal and psychiatric characteristics; their asthma histories and asthma severity; features of medical and personal management; circumstances surrounding the fatal or near-fatal episode; and whether the episode could have been prevented.

The study period was from May 1988 to June 1991. Persons dying in South Australia during this period were enrolled in the study if 'asthma', 'asthmatic' or 'status asthmaticus' was recorded in Part 1 or II of the death certificate. The death certificates then were reviewed and if the death *may* have been due to asthma, the certifying doctor was interviewed concerning the circumstances surrounding the death. Interviews were then held with the cases' general practitioners, allied health professionals and household or other close acquaintances.

During the same period, NFA cases presenting to accident and emergency departments of Adelaide teaching hospitals were recruited. To be eligible

for entry into the study, cases had to have experienced asthma resulting in either respiratory arrest, or a $PaCO_2$ above 50 mmHg and/or an altered conscious state or inability to speak on presentation to hospital. Interviews of an identical format to those for death cases were held with household or other close acquaintances and general medical practitioners.

This study shows that asthmatics dying from asthma share many important similarities with those asthmatics who survive a near-fatal attack. This applies to: the severity of their asthma; the frequency of asthma symptoms; the impact of asthma on school or work attendance; histories of asthma episodes leading to visits to hospital accident and emergency departments, general hospital admissions and admission to intensive care units; the type of primary health care provider; histories of lung-function testing; use of crisis plans; compliance with prescribed medication; and quality of medical management. Help-seeking behaviour during the fatal or near-fatal episode appeared to be similar and histories of previous psychiatric consultation and levels of psychiatric caseness were also similar.

The asthma death and NFA cases included in the present study were not similar in all respects. NFA cases tended to be younger, to include more males, to be less likely to have concurrent medical conditions, to be more likely to have high levels of denial, to have made fewer doctor visits for asthma in the 12 months prior to the attack, and to have made less use of asthma medications in general.

There were 80 cases in the asthma death group and 154 cases in the NFA group. The death cases were significantly older (mean age 52.3 years, and for the near-fatal attack group 36.1 years). Males comprised 39% of deaths and 57% of the NFA group. These differences were significant.

The levels of asthma severity found in this study were similar to those found in previous studies; 73% of asthma death cases and 65% of NFA cases were classified as having severe asthma, compared with 65% who were assessed as having severe asthma in the Victorian asthma mortality study conducted in 1986.

In the present study, 39% of asthma death cases and 45% of NFA cases were reported as having been admitted to hospital in the preceding 12 months, compared with 39% of cases reported to have been admitted in the preceding 12 month period in both the New Zealand and Victorian asthma mortality studies. A history of admission for asthma in the preceding 12 months has been reported to be the strongest single indicator of

risk for subsequent death from asthma, and is also an indicator of subsequent risk for readmission.

The Victorian asthma mortality study reported that 65% of cases (n = 193) had been provided with an appropriate asthma management plan, compared with 37% of asthma death cases and 49% of NFA cases in the present South Australian asthma mortality study. Only 31% of asthma death cases and 38% of NFA cases were reported as having used a peak flow meter at home, which is not significantly different from the proportion (31%) previously reported amongst asthmatics attending accident and emergency departments in 1992. Only 13 of 163 cases were reported to have had a peak expiratory flow meter in the Victorian asthma mortality study performed in 1986.

Prior medical management was assessed as optimal in only 25% of asthma death and NFA cases combined, with no significant difference between the two groups, on the basis of a consensus opinion of a reviewing committee. The perception of the quality of the medical management was extremely difficult to distinguish, however, from the quality of personal asthma management. Individual self management was assessed as poor for 53% of asthma death cases and 67% of NFA cases. However, when the analysis was restricted to subjects aged less than 60 years, similar levels of poor self management were seen for both groups. Reported compliance with prescribed medication from general practitioner reports was similar for the two groups (69% and 58% respectively).

That 53% of asthma death cases and 45% of NFA cases in the present study were regularly using beta agonists without concomitant preventive medication gives cause for concern. The corresponding figure for the Victorian asthma mortality study was 41%. Regular use of oral corticosteroids were reported for 26% of the asthma death and 16% of the NFA cases, with a figure of 16% also applying in the Victorian asthma mortality study, compared with 42% in the New Zealand study from the early 1980s and 69% in the British study from the late 1970s.

Reportedly, 16% of asthma death cases and 24% of NFA cases had purchased medications (inhaled beta agonists) directly from the pharmacist without a doctor's prescription. Asthmatics who purchase beta agonists directly from the pharmacist have been shown to be less likely to consult with family doctors and also less likely to use prescription-only medication. The high rate of repeat purchase of asthma medication on prescription without further medical consultation, as observed for asthma death (24%) and NFA

cases (42%), suggests that an opportunity for regular review and education regarding appropriate asthma treatment is not being utilised for asthmatics who have clearly experienced high levels of prior morbidity due to asthma.

Delay in seeking medical care was a feature of the final event for 56% of asthma deaths and 58% of NFA cases. Delay in receiving medical care was more common in the asthma death group than the NFA group. Amongst those cases where the final event was considered either definitely or probably preventable, delay in actually receiving medical care and less ready access to acute medical care distinguished death cases from NFA cases.

Asthma education will need to provide asthmatics with skills to recognise deteriorating control of asthma, and with appropriate strategies to manage the deterioration. At present, many asthmatics appear just to increase the use of inhaled beta agonist therapy, adopting a 'wait and see' approach hoping the situation will improve. It is of concern that in response to increased asthma symptoms only 20% of asthma death and NFA cases were reported to have increased use of oral corticosteroid medication in the prior 12 months, while over 80% of cases in both groups had increased the use of beta agonists.

Overall, 22% of asthma deaths in the present study were assessed as definitely having preventable factors associated, and 8% of the NFA cases were so assessed, compared with 37% of 126 asthma death cases which were assessed as definitely preventable in the Victorian study. Almost two-thirds (62%) of asthma death cases in the present study were considered definitely or probably preventable, compared with 61% of 271 cases in the New Zealand asthma mortality study, and 86% of 90 cases in the British study. A higher proportion of NFA cases (83%) was assessed as having preventable factors definitely or probably present, possibly reflecting the lower incidence of end-stage asthma in this younger group.

Reference

LEUNG, R. C., CARLIN, J. B., BURDON, J. G. & CZARNY, D., 1994. Asthma and allergy and atopy in Asian immigrants in Melbourne. *Medical Journal of Australia* 161(7): 418–425.

R. J. PIERCE

ASTHMA PREVENTION AND TREATMENT

Asthma is a disease of the airways—the branching system of tubes through which we draw air into the lungs, where exchange of oxygen and carbon

dioxide with the blood and tissues occurs. The fundamental abnormality in asthma is inflammation of the inner lining of the airways with swelling, secretion and narrowing of the lumen and air passage. There is also contraction of the bronchial smooth muscle surrounding the airways with resultant further narrowing of the lumen.

The principles of management of asthma involve firstly the prevention and treatment of airway inflammation and secondly relaxation of the bronchial smooth muscle.

Detailed analysis of asthma deaths has revealed that many result from lack of the knowledge about the condition on the part of many patients, and inadequate treatment strategies. The National Asthma Campaign was formed with the aims of reducing the mortality and morbidity in asthma, maintaining normal airway function and a normal lifestyle for patients with asthma. Constituent bodies are respiratory physicians (Thoracic Society of Australia and New Zealand), family doctors (Royal Australian College of General Practitioners), pharmacists (Pharmaceutical Society of Australia) and the Asthma Foundations of Australia.

The aims of asthma management are to minimise symptoms, to maximise lung function and maintain function at its best at all times, identify trigger factors and prevent the development of permanently abnormal lung function, to reduce the risk of death from an acute attack and to achieve the best quality of life for the person with asthma.

The Six Step Asthma Management Plan outlines these principles.

1. *Assess asthma severity*

Assess lung function when the condition is stable, not during an acute attack.

2. *Achieve best lung function*

Treat with intensive asthma therapy until the 'best' lung function is achieved as shown by measurement of spirometry or PEF.

3. *Maintain best lung function — avoid trigger factors*

Identify and avoid trigger factors and inappropriate medications. Peak flow monitoring can be helpful here.

4. *Maintain best lung function with optimal medication*

Treat with the least number of medications and use the minimum doses necessary.

Ensure the patient understands the difference between 'preventer' medications which combat inflammation and 'reliever' which relax bronchial smooth muscle.

Take active steps to reduce the risk of adverse effects.

5. *Develop an action plan*

Discuss and write a plan for the management of exacerbations.

Detail the increases in medication doses and when and how to gain rapid access to medical care.

6. *Educate and review regularly*

Ensure patients and their families understand the disease, the rationale for their treatment and how to implement their action plan.

Emphasise the need for regular review, even when asthma is well controlled.

The concept of the individual asthmatic person taking an active role in the management of his or her condition as part of a team effort with their local doctor and pharmacist is very important in successful management. The best patient outcome is most likely to be achieved when there is a close working relationship between an interested doctor and an informed patient.

BRUCE KNOX

POLLEN AND THE WEATHER

Pollen grains occur in conifers and flowering plants and carry the male gametes. They are released into the air for fertilisation so that pollen is a natural component of the atmosphere in all seasons, but is especially numerous in spring and early summer in temperate climates. Susceptible humans, breathing the pollen-laden air, develop the symptoms of hay fever and asthma. These allergic diseases are triggered by the presence of certain proteins and glycoproteins in some kinds of pollen that act as allergens. These are environmental proteins or glycoproteins, which interact with the human immune system and trigger the allergic response. Given the dramatic increase in incidence of allergic disease that has occurred during the past 30 years, there has been increasing public concern about allergenic pollen. In this talk, we will examine when, where and in what quantities pollen allergens are present in the aerial environment and how it is affected by weather patterns.

Assessment of the amount of pollen in the air is obtained through use of spore traps, which provide quantitative incidence estimates per cubic metre of air sampled on an hourly to annual basis, as levels of efficiency depending on the size of the particle. A pollen calendar has been produced for Melbourne which shows this information graphically for 22 different types of pollen. Tree pollens predominate in winter: ash, birch, olive and wattle are the most allergenic in humans and, with the exception of wattle, are exotic horticultural species. In spring and early summer, grass pollen predominates (26% of the total pollen catch in Melbourne). Grass pollen is the major source of aeroallergens in the external environment, with about 60% of allergic humans being sensitised to this type of pollen. Weed pollens follow in summer, e.g. wall pellitory, which is now the dominant weedy plant in the CBD of Sydney and abundant in central Melbourne.

The seasonal total pollen counts vary widely from season to season, reflecting the intensity of flowering in any year. For Melbourne, the range is from 2319 to 8217 grains m^{-3} $year^{-1}$, similar to cities in Europe with temperate climates. The key factor regulating the seasonal appearance of grass pollen allergens is average temperature, which is precisely correlated with increasing grass pollen counts. This relationship can be used to predict the intensity of the pollen season. In Melbourne, wind direction is important, with northerly and northwesterly winds carrying high levels of grass pollen.

Rainfall during winter can be used as a predictor for the onset of the grass pollen season. Rain is negatively correlated, since the pollen is washed out of the air. Hay fever sufferers can breathe easy, but not so asthmatics. Rainfall merely changes the total allergen load in the atmosphere, causing the pollen allergens to disperse into the atmosphere aerosol. They exist in two different forms, allergen molecules and allergen-containing fine particles. As grass pollen grains remain living cells for only about one hour after entry into the atmosphere, most grains will be dead. In this condition, they are assumed to behave like a sponge in which allergen molecules diffuse from microchannels in the outer walls from the grains when moistened and become dispersed in the aerosol. Allergen-containing fine particles (starch granules) are produced when grains rupture osmotically during rainfall and are released from the single pore into the atmospheric aerosol. There are approximately 700 of these fine particles in each grain and their size ranges from 0.6 to 2.5 μm. In Melbourne on days following rainfall, a 50-fold increase in the number of particles m^{-3} air has been reported. Allergenic starch granules have been associated with epidemics of thunderstorm asthma during the grass pollen season.

A consequence of the release of allergen molecules into the aerosol is that these molecules are free to interact with other types of fine particles that are associated with air pollution. For example, diesel emitted carbon particles (DECP), each 60 nm in size but forming into fractal aggregates, originate from diesel engine exhaust emissions. Such fine particles have recently been shown to have serious health risks in several American cities with polluted air. These DECPs can become loaded with grass pollen allergen molecules, effectively concentrating the allergens, and suggesting a causal mechanism for the increased levels of asthma in cities during episodes of air pollution. Starch granules are, however, the only class of fine particles that have been tested clinically to show they are capable of eliciting an attack of asthma. There is now a need for quantification of the relative allergenic activities of these various fractions of grass pollen allergens and their contribution to the allergenic activity of the atmospheric aerosol.

1321