PROCEEDINGS
of the
LINNEAN SOCIETY
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NEW SOUTH WALES

VOLUME 110
NUMBER 1
NUMBER 2

NATURAL HISTORY IN ALL ITS BRANCHES

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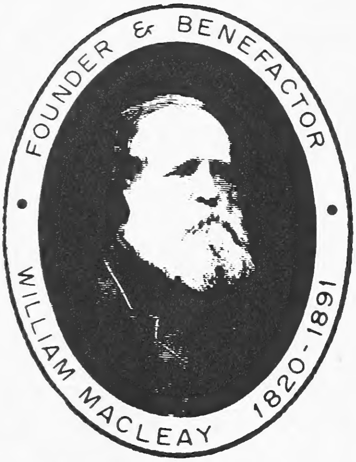

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Cover motif: 'Fossils of Talbragar', a vignette designed and drawn for this volume by Alan E. J. Andrews.

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Diurnal Survey of Ichthyoplankton Abundance, Distribution and Seasonality in Botany Bay, New South Wales

ALDO S. STEFFE and BRUCE C. PEASE

STEFFE, A. S., & PEASE, B. C. Diurnal survey of ichthyoplankton abundance, distribution and seasonality in Botany Bay, New South Wales. *Proc. Linn. Soc. N.S.W.* 110 (1), (1987) 1988: 1-10.

We found 37 types of pelagic eggs, and 27 taxa of fish larvae representing 12 families, during an ichthyoplankton survey in Botany Bay from September 1977 to October 1979. A small plankton net was used to take surface samples during the day. Pelagic eggs were most abundant during February (late summer) of both years. The abundance of pelagic eggs decreased significantly with increasing distance into the estuary from the bay entrance. The greatest number of larval fish taxa was captured in March (early autumn) of year 1. Although Botany Bay is physically best termed an ocean embayment, its larval ichthyofauna is similar to that of other temperate estuaries worldwide, in that larvae derived from demersal eggs dominated the assemblage. Larvae hatched from demersal eggs contributed more than 78% of all larvae collected. The percentage of larvae derived from demersal eggs at each station increased significantly with increasing distance into the estuary.

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KEY WORDS: Ichthyoplankton, fish larvae, pelagic eggs, distribution, seasonality, Botany Bay, temperate estuary, ocean embayment.

INTRODUCTION

The only published study of ichthyoplankton in an Australian estuary is that relating to the Blackwood River estuary in Western Australia (Lenanton, 1977). Eggs and larval stages of some Australian marine fish species have been described (Tosh, 1902, 1903; Dakin and Colefax, 1934, 1940; Munro, 1942, 1945, 1948, 1953, 1955; Thomson and Bennett, 1953; Cassie, 1956; Thomson, 1963; Robertson, 1973, 1975; James, 1976; Leis and Rennis, 1983) but there is still little Australian ichthyological literature in the fields of egg and larval development, and estuarine ichthyoplankton ecology.

Our object was to describe the ichthyoplankton assemblage of Botany Bay, New South Wales, and to compare the findings with those from other temperate estuaries worldwide.

MATERIALS AND METHODS

Study Area

Botany Bay (34°01′S, 151°11′E) is a large, semi-landlocked estuary (Fig. 1). The bay has a surface area of 4160ha and receives discharge from the Georges and Cooks Rivers. Despite this riverine influence the bay is dominated by ocean swell and wind waves (Roy *et al.*, 1980), is vertically well mixed (Rochford, 1951), and at most times is best described as a marine embayment. The bay has extensive areas of seagrasses and mangroves.

Definitions

Ichthyoplankton: portion of fish community found in the plankton and which have not attained juvenile status.

Larval assemblage: all larvae caught within the constraints of the sampling programme. That is, by daytime sampling within three hours of high tide.

The terms pelagic egg, demersal egg, larva, and juvenile all follow the definitions of Leis and Rennis (1983).

In Botany Bay the families Gobiidae, Blenniidae and Syngnathidae which is ovoviviparous were considered to have demersal eggs, and all other taxa were regarded as having pelagic eggs.

Year 1: September 1977 to August 1978 inclusive.

Year 2: September 1978 to August 1979 inclusive.

Taxon diversity: number of taxa present at all stations during a given month. Taxa identified to family level are only regarded as a single unit. Taxon diversity was not calculated when only unidentifiable yolk-sac and damaged larvae were represented that month.

Collection of Samples

Plankton samples were collected at nine stations each month from September 1977 to May 1978 then from August 1978 every second month to October 1979 (Fig. 1). A further station, Mangrove Channel (MC, Fig. 1), was sampled only until October 1978.

A 27.5cm diameter net with 350μm mesh was used for the monthly samples to May 1978 when it was lost. A net with mouth diameter of 40cm and the same mesh size was used thereafter. The 40cm diameter net which filtered about twice as much water as the first net was used for the rest of the study. All ichthyoplankton counts from samples collected with the 27.5cm diameter net were doubled to account for the increased filtering capacity of the second net.

At each station two replicate samples were collected. All sampling was carried out around high tide (± 3hrs) during daylight. The plankton net was towed for five minutes (± 5secs) at the surface at a speed of approximately 1.0m sec^{-1}. Although a flowmeter was not used to quantify the amount of water filtered the towing speed for each sample was kept the same by setting the number of engine revolutions at a constant value. Immediately after collection all plankton samples were preserved in 10% buffered formalin. All samples were sorted entirely, using a dissecting microscope. Larvae were identified using the size series method (Leis and Rennis, 1983) and pelagic egg types were identified using the characters outlined by Robertson (1975).

Equipment failures and inclement weather sometimes prevented completion of the full sampling programme for a given month. No stations were sampled during June 1978. Stations not sampled at other times were the Northern Bay (September 1977), Mangrove Channel (March 1978), Towra Point (August 1978), Woolooware Bay and Georges River (October 1978), and North-Central Bay (April 1979).

RESULTS

Limitations of Data Set

The limitations of the data set this manuscript is based on can be summarized as follows:

1. Individual sample sizes, i.e. the volume of water filtered per tow, appear to be too small. In order to rectify this we decided to pool samples. Pooling enabled us to increase sample sizes to an acceptable level but decreased the available degrees of freedom for

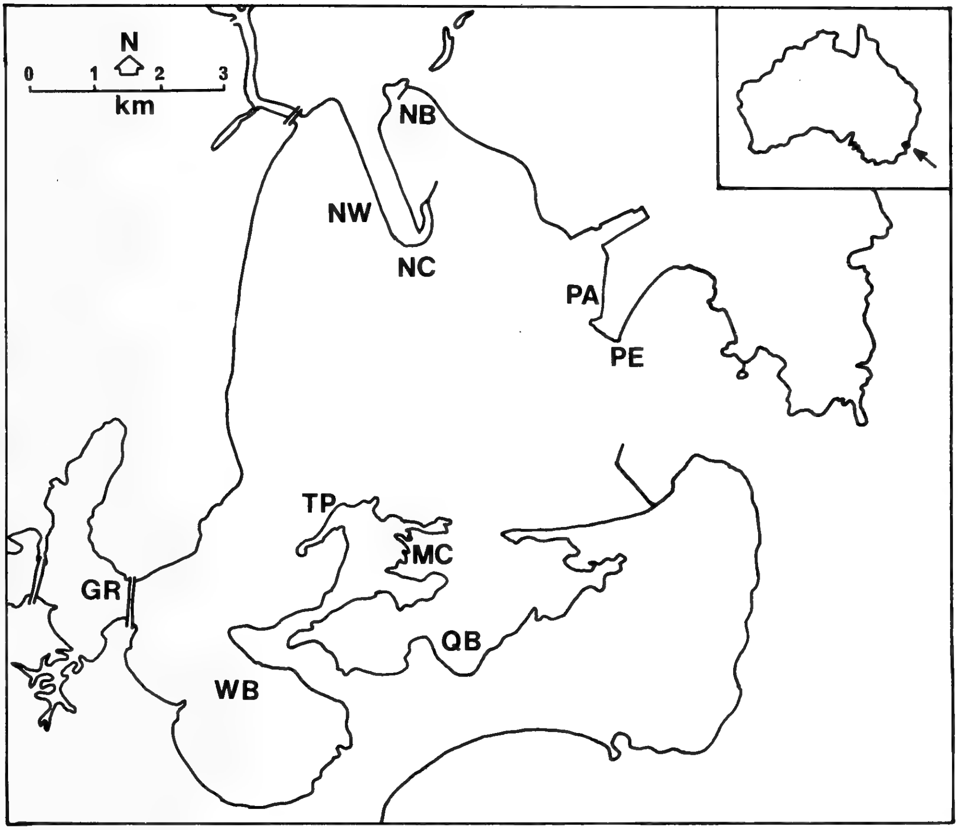

Fig. 1. Location of sampling stations in Botany Bay. Abbreviations are: PE = Port Entrance, PA = Port Area, NC = North-Central Bay, QB = Quibray Bay, NW = North-West Bay, TP = Towra Point, NB = Northern Bay, WB = Woolooware Bay, GR = Georges River, MC = Mangrove Channel

statistical tests. Therefore the trends we observed must have been strong because the fewer samples the more marked a trend must be to give a significant result.

2. Larval avoidance of the small nets was potentially large. We resolved this dilemma by restricting our survey to pelagic eggs and early larval stages which our nets sampled adequately.

3. Although we acknowledge the larval assemblage would have been better estimated using larger nets, and by sampling at night we believe our samples represent accurately the relative proportions of early stage larvae hatched from demersal, and pelagic eggs present in the larval assemblage.

Species Composition

The pelagic eggs collected were found to comprise 37 types, however, only the oval egg of the anchovy *Engraulis australis* could be identified with certainty.

Twenty-seven taxa of larvae from 12 families were collected (Table 1). The bulk of the larval assemblage were species from demersal eggs (78.9%), with Gobiid and Blenniid larvae being the most abundant.

Spatial Distribution of Ichthyoplankton

Pelagic eggs were most abundant at the two stations nearest the entrance with the Port Entrance and Port Area stations (Fig. 1) accounting for over 76% of all eggs collected (Table 2). The abundance of pelagic eggs (logarithmically transformed) decreased significantly with increasing distance into the estuary from the Bay entrance (Fig. 2**a**).

Larvae from demersal eggs were dominant in the catch at all sites except the Port Entrance. The percentage of larvae from demersal eggs at each station increased significantly with increasing distance into the estuary (Fig. 2**b**).

Seasonal Abundance

In both Year 1 and Year 2 the peak in abundance of pelagic eggs occurred in February (Fig. 3).

Larval fish catches in excess of 40 were recorded during October, November, February and March of Year 1; and February of Year 2 (Table 1). The October peak in Year 1 is due to a catch of 108 individuals of goby species 4 at Woolooware Bay.

Larval fish abundances in Year 1 peaked during October-November (Spring) and February-March (late Summer-early Autumn), whilst during Year 2 only the February (late Summer) peak was repeated (Table 1).

Taxa Diversity of Larvae

Four taxa of larvae or more were caught in October, November (Spring) and January, February, and March (late Summer — early Autumn) of Year 1 and December, February, April (Summer Autumn), and August (Winter) of Year 2 (Table 1). Taxa diversity was low at other times.

The diversity of fish larvae we found was extremely low compared with the total of 229 species of fish recorded from Botany Bay during the same period (Anon, 1981).

DISCUSSION

Whilst we acknowledge that the data set is limited due to some problems associated with the collection procedures (see Results) we believe that this survey is representative of the pelagic egg and early stage larval component of the ichthyoplankton. We interpret the large proportion of pelagic eggs found near the bay's entrance and the observed

TABLE 1

Seasonal Abundance and Taxon Diversity of Fish Larvae (All Stations Pooled)

TAXA	1977				1978								1979				
(arranged in taxonomic order)	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Aug	Oct	Dec	Feb	Apr	June	Aug	Oct
Myctophidae	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—
Atherinidae	—	2	2	—	—	2	—	—	—	—	—	—	—	—	—	—	—
Syngnathidae																	
Stigmatopora argus	—	—	—	—	—	—	—	—	2	—	—	—	—	1	—	—	—
Stigmatopora nigra	—	—	2	—	—	—	4	—	—	—	—	—	—	1	1	—	—
Syngnathus margaritifer	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Urocampus carinirostris	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Yozia tigris	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sillaginidae																	
Sillago ciliata	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—
Gerreidae																	
Gerres ovatus	—	—	—	—	4	—	34	—	—	—	—	—	1	—	—	—	—
Sparidae	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—
Monodactylidae																	
Monodactylus argenteus	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—
Kyphosidae																	
Girella tricuspidata	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mugilidae																	
Liza argentea	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Blenniidae																	
Omobranchus anolius	—	—	16	4	6	22	14	—	—	—	—	5	10	1	—	—	—
Petroscirtes lupus	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—
Gobiidae (4 spp.)	10	118	22	4	24	36	24	—	—	—	3	11	27	1	—	2	4
Monacanthidae																	
Meuschenia sp.	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—
Unknown taxa (7 spp.)	—	6	—	2	—	2	4	—	—	—	—	—	1	1	—	5	—
Unidentifiable yolk-sac and damaged larvae	—	—	—	—	2	—	16	—	—	1	—	—	3	—	—	—	—
Total No. larvae	14	128	44	10	36	62	102	2	4	1	3	17	42	6	1	7	5
Taxon Diversity	3	7	6	3	5	6	10	1	2	0	1	4	6	6	1	5	2

TABLE 2

Total Abundance of Ichthyoplankton and Percentage of Larvae from Demersal Eggs at Each Station

Station	Distance from entrance (kms)	No. Pelagic Eggs	No. Larvae	% Larvae from Demersal Eggs
Port Entrance	2.5	1472	13	38.5
Port Area	4.0	874	24	66.7
North-Central Bay	5.9	208	18	66.7
Quibray Bay	7.1	123	14	85.7
North-West Bay	7.4	51	56	58.9
Towra Point	7.5	155	113	85.8
Northern Bay	7.6	147	54	63.0
Woolooware Bay	11.1	24	153	94.8
Georges River	11.3	27	31	83.9
Mangrove Channel*	6.1	4	8	25.0

*Station Excluded from Regression Analyses as sampling was discontinued after October 1978.

decline in numbers further into the estuary ($p<0.001$) to be due to most species with pelagic eggs spawning near the bay entrance or outside the estuary (Bell, 1980), and, the subsequent 'dilution' of pelagic eggs within the estuary by localized tidal and wind currents.

Although Botany Bay is characterized by its marine qualities (Roy *et al.*, 1980) it has a larval assemblage dominated by taxa of estuarine origin, i.e. larvae hatched from demersal eggs.

No apparent trend was found between distance from the bay entrance and the abundances of larvae derived from pelagic eggs, or those hatched from demersal eggs. However, there was a change in the relative proportions of these larvae with increasing distance into the estuary. The percentage of larvae derived from demersal eggs at each station increased with distance into the estuary ($p<0.02$). This trend is not surprising as most species with pelagic eggs spawn outside the bay or near the entrance (Bell, 1980), and many species with demersal eggs spawn within Botany Bay (Bell *et al.* 1984, Middleton *et al.* 1984).

Because larvae from demersal eggs hatch at an advanced stage of development, with a better swimming capability than comparable larvae from pelagic eggs they are more likely to be retained within the estuary. Thus the earlier stages of larvae hatched from pelagic eggs could be present in Botany Bay only in low numbers, with active migration into the estuary probably occurring later, at larger sizes which were capable of avoiding our small nets. The February peaks in abundance of pelagic eggs correspond with the late Summer peak in spawning of economically valuable fish species found by Bell (1980) in Botany Bay. The peak of pelagic eggs in February of Years 1 and 2, the larval species diversity peak in March of Year 1, and a subsequent large catch of larvae in mid-March 1981 (Steffe, 1982) suggest that the peak spawning period of most fish (including those of no economic importance) in the bay occurs in late Summer (February) — early Autumn (March). Whilst Botany Bay has been shown to be an important transitory nursery area for many commercially valuable fish species (Bell, 1980; Anon, 1981; Bell *et al.*, 1984; Middleton *et al.*, 1984) it appears that relatively few of these species utilize Botany Bay during all phases of their life cycle.

Although the Botany Bay estuary is, physically, best termed an oceanic embayment, its larval assemblage closely resembles the estuarine larval ichthyofaunas of other temperate regions. In Botany Bay, larvae hatched from demersal eggs constituted 78.9% of the larval ichthyofauna with the Gobiidae being the most abundant taxa. Similarly, the larval assemblages of other temperate estuaries in Western Australia,

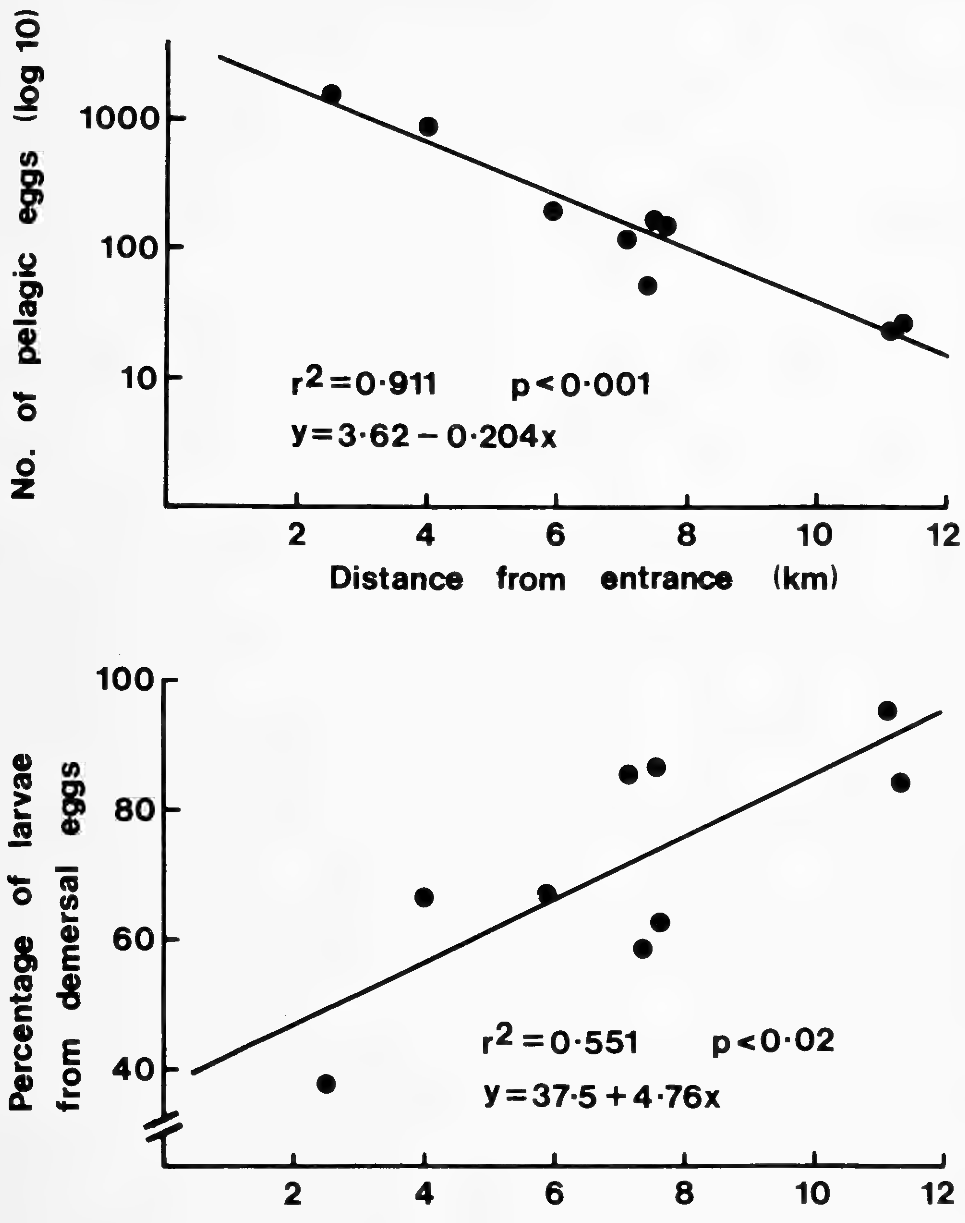

Fig. 2 **a** (top). Regression line and equation for the number of pelagic eggs ($\log_{10}$) against distance from the Bay entrance. **b.** Regression line and equation for the percentage of larvae from demersal eggs at each station against distance from the Bay entrance.

North America and South Africa are also dominated by species hatched from demersal eggs. The species from demersal eggs component of the Blackwood River estuary larval ichthyofauna exceeded 83%, with the Gobiidae also dominating (Lenanton, 1977).

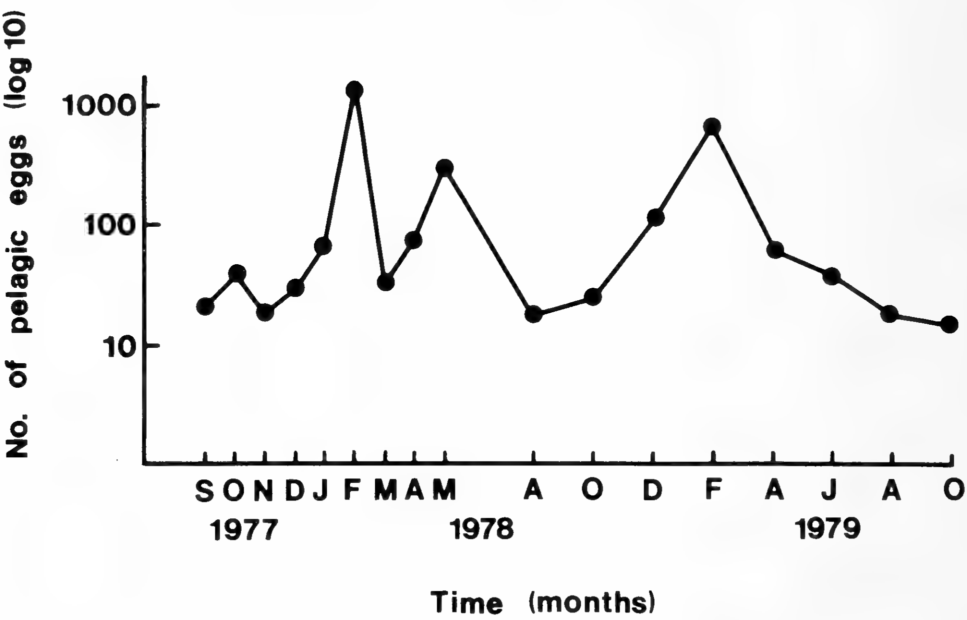

Fig. 3. Seasonal abundance of pelagic eggs (all stations pooled).

Pearcy and Richards (1962) found that in the Mystic River estuary, Connecticut, species from demersal eggs comprised 97% of all larvae collected. Similarly, the contribution of species from demersal eggs to the larval ichthyofaunas of Yaquina Bay, Oregon (Pearcy and Myers, 1974), and the estuaries of central Maine (Chenoweth, 1973) were in excess of 90% and 95% respectively. Species from demersal eggs constituted over 97% of the larval ichthyofauna of the Swartkops estuary (Melville-Smith and Baird, 1980) and more than 96% of the larval assemblage of the Kromme River estuary, South Africa (Melville-Smith, 1981).

Melville-Smith and Baird (1980) noted that the dominant larval species in the North American studies and their Swartkops estuary work were all members of the Gobiidae and Clupeidae. They suggested that this could be 'indicative of parallel niche evolution of the dominant Gobiidae and Clupeidae in the two areas'. However, we believe that the observed similarities between North American, South African and Australian temperate estuarine larval ichthyofaunas reflect the demersal reproductive strategies employed by the adult populations. Demersal eggs are relatively large, heavily pigmented, have long incubation periods, and produce well-developed larvae. The reverse is true of pelagic eggs. Demersal eggs have minimal exposure to fluctuations of salinity and temperature, which are more pronounced in surface waters, because of their location on or near the substrate. The large expenditure of energy on individual egg production in species with demersal eggs enhances larval survival by shortening the susceptible early planktonic period. Thus, at the time of hatching, larvae from demersal eggs are better able to forage for food, and to maintain their position within the estuary. We believe that a response to selective pressures at the egg stage produces better adapted larvae for the estuarine plankton environment. In our opinion dominance of species from demersal eggs in the temperate estuarine ichthyofaunas reflects this.

ACKNOWLEDGEMENTS

The material for this paper was collected in conjunction with a study of fish habitat utilization in Botany Bay, which constituted part of the N.S.W. State Pollution Control Commission's study of Botany Bay. Eric van der Wal designed and constructed the nets and initiated collections. We thank J. Story for help with collection and sorting of samples and J. Leis and I. S. R. Munro for assistance in identification of specimens. Constructive criticisms of the manuscript were provided by C. Barlow, J. Bell, D. Pollard, M. Westoby and R. Williams.

References

ANON, 1981. — The ecology of fish in Botany Bay — biology of commercially and recreationally important species. State Pollution Control Commission of New South Wales Rep. No. BBS23B. Sydney.

BELL, J. D., 1980. — Aspects of the ecology of fourteen economically important fish species in Botany Bay, New South Wales, with special emphasis on habitat utilisation and a discussion of the effects of man-induced habitat changes. North Ryde, N.S.W.: Macquarie University, M.Sc. thesis, unpubl.

——, POLLARD, D. A., BURCHMORE, J. J., PEASE, B. C., and MIDDLETON, M. J., 1984. — Structure of a fish community in a temperate tidal mangrove creek in Botany Bay, New South Wales. *Aust. J. Mar. Freshw. Res.* 35: 33-46.

CASSIE, R. M., 1956. — Early development of the snapper *Chrysophrys auratus* Forster. *Trans. Roy. Soc. New Zealand* 83: 705-713.

CHENOWETH, S. B., 1973. — Fish larvae of the estuaries and coast of Central Maine. *U.S. Fish Bull.* 71: 105-113.

DAKIN, W. J., and COLEFAX, A. N., 1934. — The eggs and early larval stages of the Australian pilchard *Sardinia neopilchardus* (Steindachner). *Rec. Aust. Mus.* 19: 136-140.

——, and ——, 1940. — The plankton of the Australian coastal waters off New South Wales. *Monograph, Univ. Sydney, Dept. Zool.* No. 1: 215 pp.

JAMES, G. D., 1976. — Eggs and larvae of the trevally *Caranx georgianus* (Teleostei: Carangidae). *New Zealand J. Mar. Freshw. Res.* 10: 301-310.

LEIS, J. M., and RENNIS, D. S., 1983. — *The Larvae of Indo-Pacific Coral Reef Fishes.* Kensington, N.S.W.: Univ. N.S.W. Press *and* Honolulu: Univ. Hawaii Press.

LENANTON, R. C. J., 1977. — Aspects of the ecology of fish and commercial crustaceans of the Blackwood River estuary, Western Australia. *Fish. Res. Bull. W.A.* 19: 1-72.

MELVILLE-SMITH, R., 1981. — The ichthyoplankton of the Kromme River estuary. *Sth African J. Zool.* 16: 71-72.

——, and BAIRD, D., 1980. — Abundance, distribution and species composition of fish larvae in the Swartkops estuary. *Sth African J. Zool.* 15: 72-78.

MIDDLETON, M. J., BELL, J. D., BURCHMORE, J. J., POLLARD, D. A., and PEASE, B. C., 1984. — Structural differences in the fish communities of *Zostera capricorni* and *Posidonia australis* seagrass meadows in Botany Bay, New South Wales. *Aquatic Botany* 18: 89-109.

MUNRO, I. S. R., 1942. — The eggs and early larvae of the Australian barred spanish mackerel, *Scomberomorus commersoni* (Lacepede), with preliminary notes on the spawning of that species. *Proc. Roy. Soc. Qld* 44: 33-38.

——, 1945. — Postlarval stages of Australian fishes — No. 1. *Mem. Qld Mus.* 12: 136-153.

——, 1948. — The economic biology of the Australian Black Bream (*Roughleyia australis* Gunther). St Lucia, Qld: University of Queensland, M.Sc. thesis, unpubl.

——, 1953. — Eggs and larvae of the four-winged flying fish *Hirundichthys speculinger* (Valenciennes). *Aust. J. Mar. Freshw. Res.* 5: 64-69.

——, 1955. — Eggs and larvae of the sabre-toothed blenny *Dasson steadi* (Whitley) (Blenniidae). *Aust. J. Mar. Freshw. Res.* 6: 30-34.

PEARCY, W. G., and MYERS, S. S., 1974. — Larval fishes of Yaquina Bay, Oregon: a nursery ground for marine fishes? *U.S. Fish. Bull.* 72: 201-213.

——, and RICHARDS, S. W., 1962. — Distribution and ecology of fishes of the Mystic River estuary, Connecticut. *Ecology* 43: 248-259.

ROBERTSON, D. A., 1973. — Planktonic eggs and larvae of some New Zealand marine teleosts. Dunedin: University of Otago, Ph.D. thesis, unpubl.

——, 1975. — A key to the planktonic eggs of some New Zealand marine teleosts. *Fish. Res. Div. Occasional Pub.* No. 9.

ROCHFORD, D. J., 1951. — Studies in Australian estuarine hydrology. I. Introductory and comparative features. *Aust. J. Mar. Freshw. Res.* 2: 1-116.

ROY, P. S., THOM, B. G., and WRIGHT, L. D., 1980. — Holocene sequences on an embayed high-energy coast: an evolutionary model. *Sedimentary Geology* 26: 1-19.

STEFFE, A. S., 1982. — The larval fish assemblage of Botany Bay — the effects of tidal and diel factors. Kensington, N.S.W.: University of N.S.W., M.Sc. (qualifying) thesis, unpubl.

THOMSON, J. M., 1963. — Synopsis of biological data on the grey mullet *Mugil cephalus* (Linnaeus). *Fish. Synopsis C.S.I.R.O. Div. Fish. Ocean.*: 54 pp.

——, and BENNETT, A. E., 1953. — The oyster blenny, *Omobranchus anolius* (Valenciennes, Blenniidae). *Aust. J. Mar. Freshw. Res.* 4: 227-233.

TOSH, J. R., 1902. — On the common whiting of Moreton Bay (*Sillago bassensis*). *Proc. Roy. Soc. Qld* 17: 175-184.

——, 1903. — Notes on the habits, development etc., of the common food fishes of Moreton Bay. *Qld Dept. Mar. Rep.* 1902-03.: 36 pp.

Two new Species of *Glycaspis* (Homoptera: Spondyliaspididae) from potentially endangered *Eucalyptus* Species, and one from *E. stricta*

K. G. CAMPBELL and K. M. MOORE

CAMPBELL, K. G., & MOORE, K. M. Two new species of *Glycaspis* (Homoptera: Spondyliaspididae) from potentially endangered *Eucalyptus* species, and one from *E. stricta*. *Proc. Linn. Soc. N.S.W.* 110 (1), (1987) 1988: 11-17.

Four rare and endangered species of *Eucalyptus* L'Hérit. and one species of relatively limited occurrence which may be threatened in the near future, have been examined for associated species of Psylloidea. Three new species of *Glycaspis* Taylor including a gall-former from *E. stricta* Sieb. ex Spreng. are described and figured. Some alterations to the present phyletic groupings of *Glycaspis* are based on some of the specimens studied.

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INTRODUCTION

Thirty-one species of endangered or potentially threatened species of *Eucalyptus* L'Hérit. (Pryor, 1981) in all mainland states of Australia were previously sampled for species of Psylloidea which might be utilizing them as host (Moore, 1970, 1977, 1983, 1984, 1985). A further five species of eucalypts listed by Pryor have now been sampled for Psylloidea, and particularly for specimens of *Glycaspis* Taylor 1960, by N. and K. G. Campbell of Sydney.

The code letters prior to each eucalypt species in this paper are those used by Pryor and Johnson (1971, 1981).

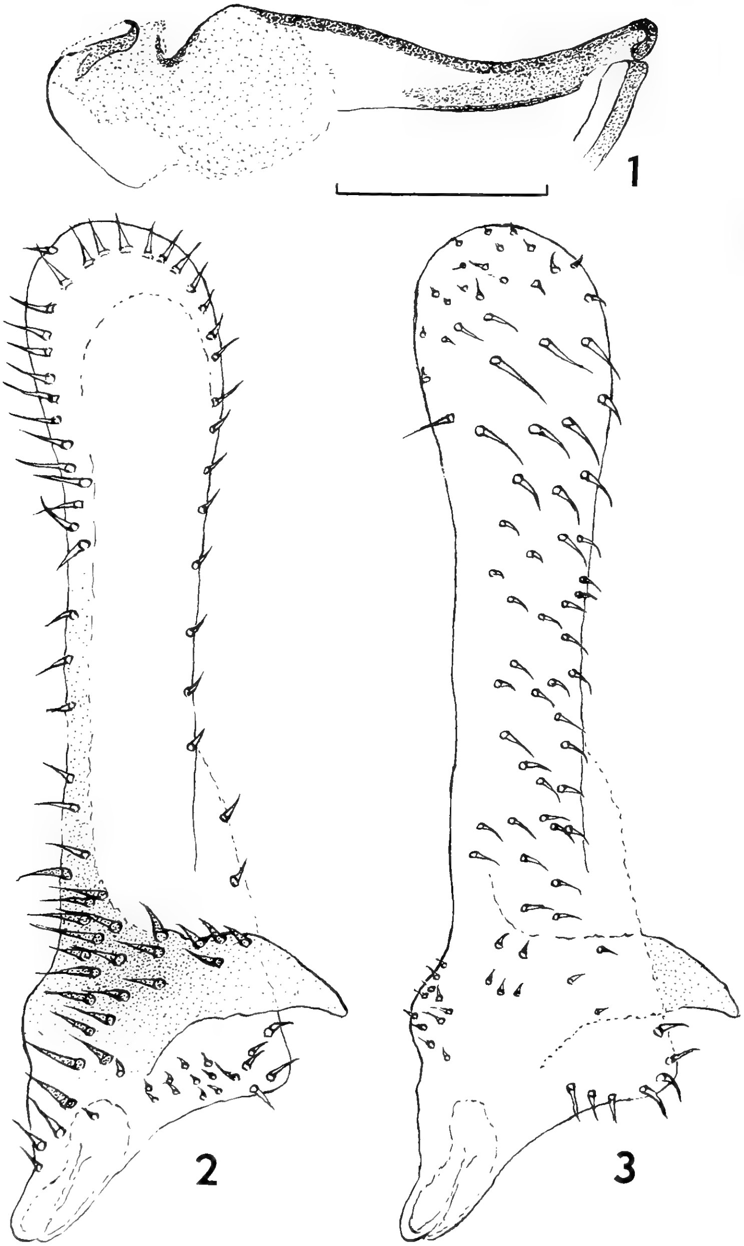
Four of the eucalypts sampled, and listed by Pryor as being of highly restricted occurrence and endangered or potentially endangered, are SIQ:A *E. squamosa* Deane and Maiden, MOKDB *E. luehmanniana* F. Muell., MOHCE *E. camfieldii* Maiden and MOKIF *E. burgessiana* Johnson and Blaxell. MOKIJ *E. rupicola* Johnson and Blaxell is listed by Pryor as being of relatively limited extent and may be threatened in the near future.

The former three species occur on the Hawkesbury Sandstone formation in the vicinity of Sydney, and the latter two species in the Blue Mountains area some 40-110km west of Sydney.

A species not listed by Pryor, MOKIG *E. stricta* Sieb. ex Spreng. was also sampled, and a new gall-forming species of *Glycaspis* obtained.

RESULTS

Three new species of *Glycaspis* are described and figured; one gall-former and one round lerp-former of subgenus *Synglycaspis* Moore 1970 together with one round lerp-former of subgenus *Glycaspis*. All specimens recorded in this paper are in the Australian National Insect Collection, CSIRO, Canberra. Psylloidea of genera other than *Glycaspis* have been referred to psyllid taxonomist K. L. Taylor for study.



Figs 1-3. Glycaspis constricta sp.n. 1, aedeagus; 2, clasper, internal face; 3, clasper, external face. Anterior edge of claspers on right. Scale line 0.1mm.

DESCRIPTIONS AND NOTES

Glycaspis (Synglycaspis) constricta sp.n.

Figs 1-3

Types: Holotype ♂ on slide labelled Kings Tableland, N.S.W., 3 vii 1985, N. and K. Campbell, *E. stricta*, 3.2km along road. Paratypes, 3 slides of single wholemount ♂♂, and 10 ♀ ♀ in 90% ethanol in tube, with same label data; 2 ♂ ♂ on slides and 2 ♀ ♀ in ethanol, with same label data except date which is 30 x 1985. All ex galls.

General colour: females orange with posterior half of forewings suffused yellow which is less intense in male specimens. Claspers and aedeagus as in Figs 1-3. Length of aedeagus 0.297-0.317mm (6 specimens).

Notes: The phyletic position of *G. constricta* is in the *brunosa* group (Moore, 1983) and appears to be nearest to *G. perthecata* Moore from which it differs in the following characters: the distal end of the aedeagus is generally on a lower plane in relation to the total length (Fig. 1), the proximal end is not as sharply curved upward; the strong setae situated posterior to the large spine on the internal face of the claspers are more numerous (Fig. 2), there are fewer setae on the large spine, anterior angle of the 'foot' of the claspers is usually at about 90° to the vertical plane, distal end of claspers broader. The host plant is MOKIG *E. stricta* while that of *G. perthecata* is MOTKA *E. haemastoma* Sm. Galls of this species have not been sighted.

Etymology: The Latin prefix *con-* = with; *stricta* = the name of the host plant.

Glycaspis (Synglycaspis) rupicolae sp.n.

Figs 4-6

Types: Holotype ♂ on slide labelled Sublime Point, Leura, N.S.W., 8-18 i 1986, K. G. Campbell, *E. rupicola* or *E. stricta*, round lerps. Paratypes, 4 slides of single wholemount males with same label data: 1 ♂ on slide labelled Kings Tableland, N.S.W., (Deer Park), 1 xi 1985, N. and K. Campbell, *E. rupicola*; 4 slides of males labelled Kings Tableland, N.S.W., 30 x 1985, N. and K. Campbell, *E. stricta*, 3.2km along road; 1 slide of male with same label data except date which is 3 vii 1985.

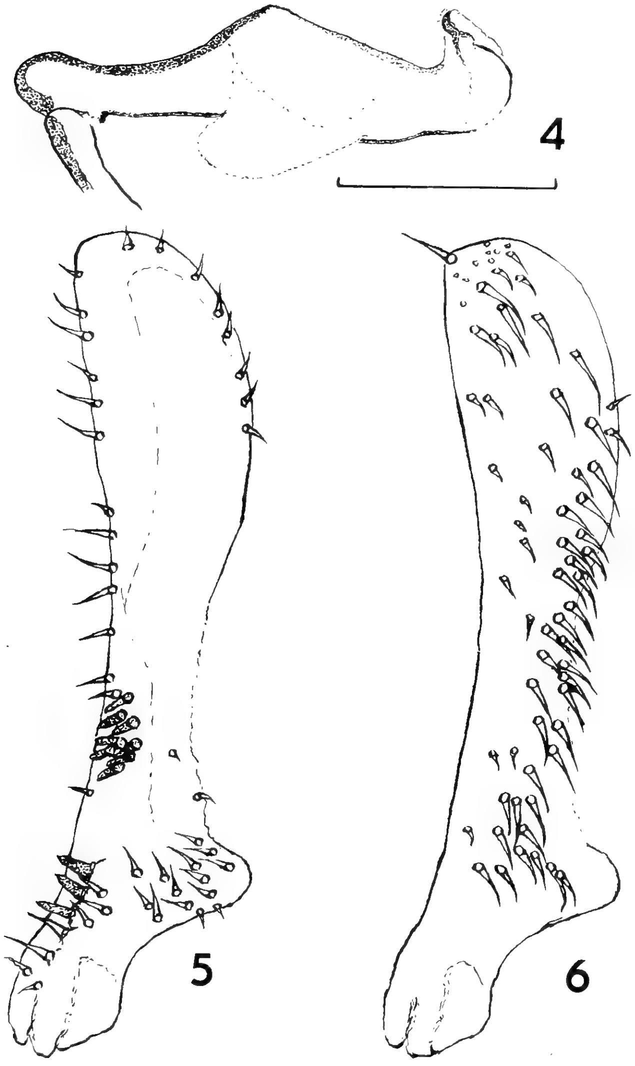
There are also 10 ♂ ♂, 15 ♀ ♀ in ethanol in tube with same label data as the holotype; 3 ♀ ♀, nymphs, lerps in tube labelled Kings Tableland, N.S.W., (Deer Park), 1 xi 1985, N. and K. Campbell, *E. rupicola*, bred from lerps; 1 ♂, 8 ♀ ♀, lerps in tube labelled Kings Tableland, N.S.W., 3 vii 1985, K. G. Campbell, *E. stricta*, 3.2km along road, bred ex round lerps, emerged 11 vii 1985; 2 ♂ ♂, 3 ♀ ♀ in tube labelled Kings Tableland, N.S.W., 30 x 1985, N. and K. Campbell, *E. stricta*. These specimens are not designated paratypes, as *G. rupicolae* and *G. cyanoreia* Moore both appear to utilize *E. stricta* and *E. rupicola* as their host, and slide material is at present necessary to separate the species.

General colour: pale cream to orange, sometimes suffused red, with dark markings. Claspers and aedeagus as in Figs 4-6. Length of aedeagus 0.231-0.251mm (8 specimens). Lerps round.

Notes: Characters on which slide material of *G. rupicolae* and *G. cyanoreia* are separable are:

G. rupicolae: proximal dorsal line of aedeagus more or less horizontal; proximal ventral line horizontal (Fig. 4); distal apex in same plane as mediodorsal expansion.

G. cyanoreia: proximal dorsal line of aedeagus strongly upturned; proximal ventral line sloping downwards; distal apex on higher plane than mediodorsal expansion (see Moore, 1970, fig. 39).



Figs 4-6. Glycaspis rupicolae sp. n. 4, aedeagus; 5, clasper, internal face; 6, clasper, external face. Anterior edge of claspers on right. Scale line 0.1mm.

G. rupicolae is placed in the *endasa* group, and appears to be nearest to *G. wallumaris* Moore from which it differs in the more pointed mediodorsal expansion of the aedeagus (Fig. 4); claspers more curved, with bases more posteriorly oriented, a group of three internal strong dark basal spines (Fig. 5), setae on external face more numerous (Fig. 6). Adults gain orange and red coloration as they feed. The host plants are MOKIG *E. stricta* and MOKIJ *E. rupicola* while that of *G. wallumaris* is MOHEJ *E. conglomerata* Maiden and Blakely, of very restricted distribution in SE Queensland.

The original description of *G. cyanoreia* (Moore, 1961:145) refers to oviposition characteristics of what now appears to be a complex of two species associated with *E. stricta* and *E. rupicola*. On the notes on that species it is stated: 'eggs occur in groups of 25 to 100, at tip, near edge or centre of leaf, but a few sometimes occur on edge of leaf. From the differences in the oviposition sites, and the male genitalia, it appears that *G. cyanoreia* and *G. rupicolae* utilize both *E. stricta* and *E. rupicola* as hosts. Detailed biological studies should separate the habits of the species.

Etymology. The name is the Latin genitive form of the host plant *E. rupicola.*

Glycaspis (Glycaspis) nancyana sp.n.

Figs 7-9

Types: Holotype ♂ on slide labelled Maroota Road, N.S.W., 23 x 1985, K. G. Campbell, *E. squamosa*, ½km SW from property J. Vigara, 1 pair *in cop.* Paratypes. 1 slide, and 4 ♀♀ in ethanol in tube with same label data; 2 slides of single wholemount males labelled Maroota Road, N.S.W., 23 x 1985, N. and K. Campbell, *E. squamosa*, ½km SW from property J. Vigara, bred ex round conical lerps, 31 x 1985; 2 ♂♂, 4 ♀♀ in tube with same label data; 1 ♂ on slide labelled Maroota Road, N.S.W., 11 ix 1985 N. Campbell, *E. squamosa*, bred ex transparent round conical lerp, 21 ix 1985, N. C.; 1 ♀, lerps, in tube with same label data; 3 ♂♂ on slides labelled Pennant Hills, N.S.W., (Sports Centre), Jan., Feb., Mar., 1986, N. and K. Campbell, *E. squamosa*; 7 ♀♀ in tube with same label data; 2 ♀♀ in tube labelled Maroota Road, N.S.W., 11 ix 1985, K. G. Campbell, sweeping.

General colour: males cream to yellow with variable dark markings, vertex and genitalia often suffused red; females similar to males but dark marks more extensive and sometimes brown or black, red suffusion more extensive, particularly on abdomen. Claspers and aedeagus as in Figs 7-9. Claspers suffused pale brown on distal one third. Length of aedeagus 0.208-0.234mm (6 specimens). Hindwing Cu_1 as Group (i) (Moore, 1970).

Notes: The phyletic position of *G. nancyana* is in the *felicitaris* group (see rearrangement of species under Phyletic Groupings). It appears to be nearest to *G. rylstonensis* Moore (with a possible affiliation with *G. fuscovena* Moore) but differing in the following characters: the aedeagus is similar in shape to that of *G. rylstonensis* but less upturned distally; claspers narrower, with anterior edge slightly concave at proximal one third, posterior edge straight from one third above base, dark suffusion on distal one third but less than on claspers of *G. fuscovena*, inner basal setae fewer in number. Lerps round

The host plant is SIQ:A *E. squamosa* of very restricted and disjunct distribution in the Sydney area, N.S.W., while that of *G. rylstonensis* is SNEEF *E. blakelyi* Maiden.

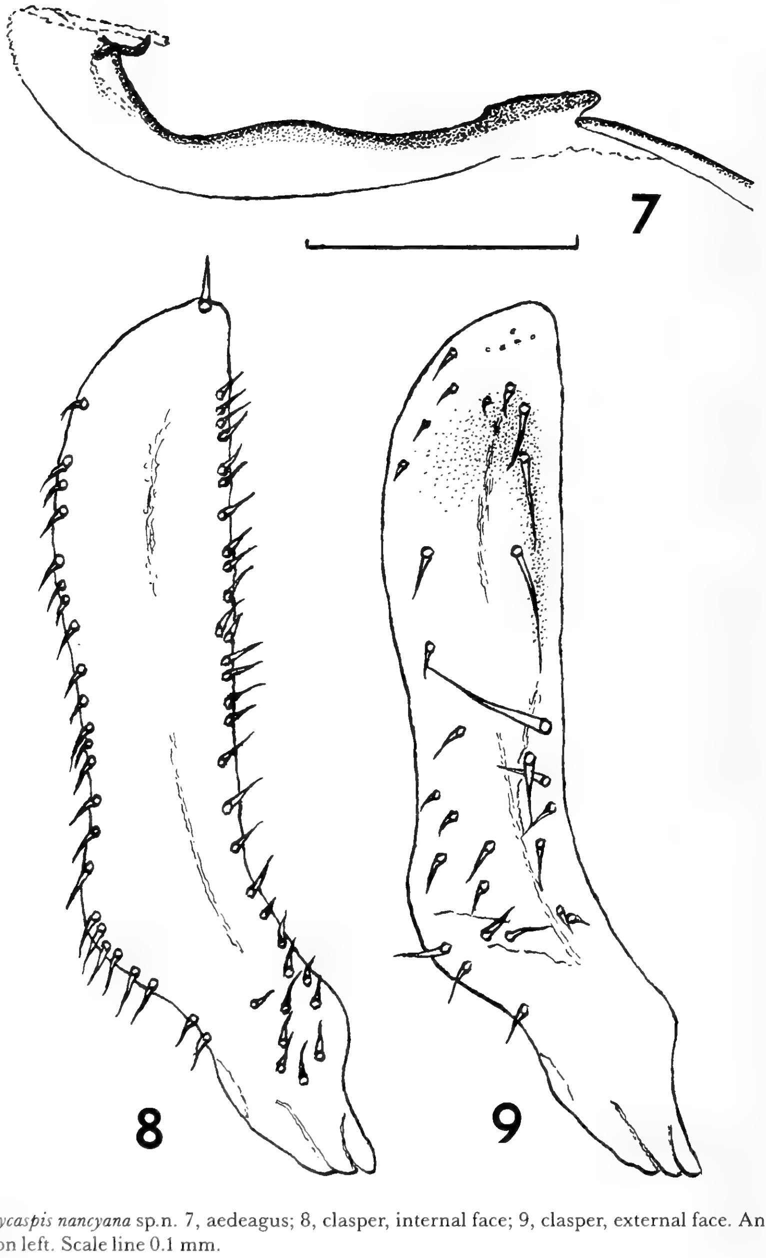
Etymology. Named for Mrs N. Campbell for her interest in, and assistance with, this project.

OTHER ***Glycaspis*** SPECIES AND NEW HOST RECORDS

Specimens of *G. conserta* Moore were obtained from *E. luehmanniana* W of Mona Vale, and from *E. burgessiana* at Faulconbridge; *G. conflecta* Moore was obtained from *E. camfieldii* at Duffy's Forest.

PHYLETIC GROUPINGS

The possible phylogeny of *Glycaspis* species was indicated in a grouping of the species (Moore, 1983). An additional group is now required to contain some of the specimens examined during this study.



Figs 7-9. Glycaspis nancyana sp.n. 7, aedeagus; 8, clasper, internal face; 9, clasper, external face. Anterior edge of claspers on left. Scale line 0.1 mm.

The *dreptodria* group of subgenus *Synglycaspis* (group 7 of Moore, 1983: 181) is reduced to the three species *G. dreptodria* Moore, *G. icterica* Moore and *G. seriata* Moore which have the aedeagus weakly upturned proximally; the six species *G. conflecta*, *G. conserta*, *G. fuliginis* Moore, *G. cyanoreia*, *G. salebrosa* Moore and *G. aggregata* Moore, now termed the *conflecta* group, have the aedeagus strongly upturned proximally; the *endasa* group consists of the five species *G. particeps* Moore, *G. hirsuta* (Froggatt), *G. endasa*

Moore, *G. wallumaris* and *G. rupicolae*, which have the aedeagus almost horizontal proximally.

The affiliations of *G. nancyana* suggest the transfer of *G. rylstonensis* from the *flavilabris* group 10 to the *felicitaris* group 9 (Moore, 1983: 182), with *G. nancyana* prior to *G. rylstonensis*, and both of these species immediately prior to *G. fuscovena*.

ACKNOWLEDGEMENTS

The authors are most grateful to Peter Weston of the New South Wales National Herbarium, Royal Botanic Gardens, Sydney, for precise locations of the eucalypt species in the field, and to Mrs N. Campbell for her assistance with the project.

References

MOORE, K. M., 1961. — The significance of the *Glycaspis* species associations with their *Eucalyptus* spp. hosts; erection of a new subgenus and descriptions of thirty-eight new species of *Glycaspis*. *Proc. Linn. Soc. N.S.W.* 86: 128-167.

——, 1970a. — A revision of the genus *Glycaspis* with descriptions of seventy-three new species. *Aust. Zoologist* 15: 248-342.

——, 1970b. — Results from a study of the genus *Glycaspis*. *Aust. Zoologist* 15: 343-376.

——, 1977. — Two new species of *Glycaspis* Taylor from Western Australia. *J. Aust. ent. Soc.* 16: 253-255.

——, 1983. — New species and records of *Glycaspis* Taylor with phyletic groupings. *J. Aust. ent. Soc.* 22: 177-184.

——, 1984. — Two new species of *Glycaspis* from tropical Queensland, with notes on the genus. *Proc. Linn. Soc. N.S.W.* 107: 475-478.

——, 1985. — Four new species of *Glycaspis* Taylor from some endangered species of *Eucalyptus*. *Proc. Linn. Soc. N.S.W.* 108: 71-78.

PRYOR, L. D., 1981. — Australian endangered species: Eucalypts. *Aust. National Parks & Wildlife Service, Special Publication* No. 5. Canberra.

——, and JOHNSON, L. A. S., 1971. — *A classification of the eucalypts*. Canberra: Aust. National University.

——, and ——, 1981. — *Eucalyptus*, the universal Australian. *In* A. KEAST, (ed.), *Ecological biogeography of Australia*. The Hague: W. Junk.

TAYLOR, K. L., 1960. — Additional information on the Australian genera of the family Psyllidae (Hemiptera: Homoptera). *Aust. J. Zool.* 8: 383-391.

Associations of some *Glycaspis* Species (Homoptera: Spondyliaspididae) with their *Eucalyptus* Species Hosts

K. M. MOORE

MOORE, K. M. Associations of some *Glycaspis* species (Homoptera: Spondyliaspididae) with their *Eucalyptus* species hosts. *Proc. Linn. Soc. N.S.W.* 110 (1), (1987) 1988: 19-24.

Host associations of some species of *Glycaspis* Taylor are correlated with the current arrangement of the genus *Eucalyptus* L'Hérit, by Pryor and Johnson. The established extent of host specificity of *Glycaspis* species is recorded.

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INTRODUCTION

The *Glycaspis* — *Eucalyptus* host associations originally were based on the eucalypt classification of Blakely, 1955 (Moore, 1961a, 1970). A more recent tentative classification of the *Eucalyptus* alliance has now been given (Pryor and Johnson, 1971, 1981; Johnson, 1976), in which the species are grouped into three suballiances consisting of nine 'subgenera'.

The genus *Glycaspis* Taylor consists of three subgenera, and relevant species — host associations are here correlated with the more recent eucalypt classification.

The hosts of the 132 species of the two more primitive *Glycaspis* subgenera are exclusively *Eucalyptus* species.

The code letters preceding each eucalypt species name in this paper are those used by Pryor and Johnson.

***Glycaspis* — *Eucalyptus* ASSOCIATIONS**

The importance of determining *Glycaspis* host associations became evident during early studies by the author on the genus *Glycaspis* in State Forests of New South Wales, when several species of *Glycaspis* and *Eucalyptus* intermingled in many discrete coastal and highland localities.

A number of the associations now known, suggest support for certain aspects of the continuing reclassification of the eucalypts by Pryor and Johnson. Examples of support are based on taxonomic and biological studies on *Glycaspis* species during more than 30 years, and reported in various papers and journals.

Examples

A. Extensive Australia-wide collections from, and observations on, more than 30 species contained in the three 'subgenera' *Angophora*, *Blakella* and *Corymbia*, have shown that *Glycaspis* species apparently do not colonize any species of the *Angophora* suballiance.

B. Species of the subgenus *Glycaspis* (*Synglycaspis*) colonize only species of the 'subgenera' *Idiogenes* and *Monocalyptus*, but not *Gaubaea*, the other 'subgenus' of the *Monocalyptus* suballiance.

C. Species of the subgenus *Glycaspis* (*Glycaspis*) colonize only species of each 'subgenus' of the *Symphyomyrtus* suballiance, namely *Eudesmia*, *Symphyomyrtus* and *Telocalyptus*.

D. The placement by Pryor and Johnson of their monotypic 'subgenus' *Idiogenes* (IAAA:A *E. cloeziana* F. Muell.) contiguous and prior to 'subgenus' *Monocalyptus* in the suballiance of the same name, is supported by *Glycaspis* (*S.*) *mactans* Moore colonizing IAAA:A *E. cloeziana*, MOG:A *E. umbra* R. T. Bak., MOG:C *E. acmenoides* Schau. and MOHEC *E. phaeotricha* Blakely and McKie (Moore, 1983: 179).

E. The inclusion of 'subgenus' *Telocalyptus* in the *Symphyomyrtus* suballiance (Johnson, 1976) is supported by the occurrence of *G.* (*G.*) *clivosa* Moore (1977) on SBA:D *E. brachyandra* F. Muell., *G.* (*G.*) *operta* Moore (1984) on SBA:C *E. raveretiana* F. Muell., and an undetermined species of *Glycaspis* (*Glycaspis*) on SSA:A *E. howittiana* F. Muell. (Moore, 1984). These eucalypts are three of the four species now grouped as *Telocalyptus*. The fourth species, SBA:A *E. deglupta* Blume, does not occur naturally in Australia, and has not been sampled for *Glycaspis* species.

The characters of the male genitalia of *Glycaspis clivosa* and *G. operta* (placed in the tropical *caurina* group of species by Moore, 1983: 183) indicate their close affinity, and probably also that of their hosts.

F. The four eucalypt species EAC:A *E. tetrodonta* F. Muell., EFAAA *E. similis* Maiden, EFC:A *E. miniata* A. Cunn. ex Schau. and EFC:B *E. phoenicea* F. Muell., of Pryor and Johnson's 'subgenus' *Eudesmia* of the *Symphyomyrtus* suballiance, are hosts for species of *Glycaspis* (*Glycaspis*) (Moore, 1970, 1984), which supports the inclusion of at least those four eucalypt species in the *Symphyomyrtus* suballiance.

Collections from seven other species of 'subgenus' *Eudesmia* have indicated that they do not seem to be hosts of *Glycaspis* species.

G. Pryor and Johnson (1981: 524) record that the eucalypt '. . . *E.* (SI) *bakeri* is related to western and central Eremaean species . . .'. This is supported by *G.* (*G.*) *inusitata* Moore (1985) colonizing *E. bakeri* Maiden at *ca*50km W of Warwick, Queensland. *G. inusitata* is included in the *deirada* group complex of species which are found mainly in Western Australia and central southern areas to Elliston, in South Australia, and on 15 hosts contained in Pryor and Johnson's Section Bisectaria which includes *E. bakeri*.

H. Pryor and Johnson (1981: 524) also record that: 'The two species of Squamosae (a Series (SIQ) of eucalypt species in Section Bisectaria), on the other hand, show no close relation with any of the trans-Eremaean species . . .'. Support is given to this finding, by *G.* (*G.*) *nancyana* Moore colonizing SIQ:A *E. squamosa* in the Sydney area of New South Wales. The closest relationship of *G. nancyana* is with *G.* (*G.*) *rylstonensis* Moore (1970) found on the solely eastern eucalypt species SNEEF *E. blakelyi* Maiden near Rylstone, New South Wales. It has no close relationship with *G.* (*G.*) *deirada* or its complex.

The second species of the Series Squamosae, SIQ:E *E. pachycalyx* Maiden and Blakely, of north Queensland, has not been sampled for possible *Glycaspis* associations.

I. Leaves of SNEET *E. brassiana* S. T. Blake were colonized by nymphs under round lerps, and adults, of *Glycaspis* (*Glycaspis*) *brimblecombei* Moore during April 1986. The small tree on which it was very prolific, was growing in the Australian National Botanic Garden, Canberra, and looked healthy. It was grown from seed collected by L. D. Pryor during April 1979, at 0.4km W of Daru Island airstrip terminal, and probably planted as seed the following spring (pers. comm. M. Carver, CSIRO, 1986).

Pryor and Johnson have placed *E. brassiana* in their Series Tereticornes which includes four known hosts of *G. brimblecombei*, namely SNEEB *E. tereticornis* Sm., SNEEF *E. blakelyi*, SNEEJ *E. dealbata* A. Cunn. and SNEEP *E. camaldulensis* Dehnh. The placement of *E. brassiana* is thus supported by the occurrence of *G. brimblecombei* on it as host.

The chemistry and metabolism of the colonized plant in Canberra would necessarily be modified by the presence or absence of certain soil chemicals and by the general environment of Canberra compared with its natural habitat of far northern Cape York and SW Papua. A similar association, of *E. camaldulensis* and *G.* (*G.*) *baileyi* Moore was reported (Moore, 1961b) in insect-host controlled colonizing experiments, the natural host being SECAC *E. saligna* Sm. The natural distributions of *E. saligna* and *E. camaldulensis* are not known to overlap in any region.

The distribution of *G. brimblecombei* is not known to be north of latitude *ca* 20°S, so it is assumed that it does not occur where *E. brassiana* grows naturally.

The following examples may be considered speculative, but seem expedient when the *Glycaspis* — host associations are considered.

J. Pryor and Johnson (1981: 525) also comment: '*E. camaldulensis* is the most widespread eucalypt, and consists of fairly different but intergrading ecogeographic races . . .'.

The three species *G. brimblecombei*, *G. blakei* Moore and *G. eremica* Moore all utilize SNEEP *E. camaldulensis* as host, in three areas each of which overlap in part, throughout the host's extensive continental distribution (Moore, 1971, 1975, 1978). This may indicate that the eucalypt species consists of three separate taxa, though two only are at present recognized.

K. In a suggested general phylogeny of the eucalypt 'subgenera' and suballiances (Johnson, 1972: 14; 1976: 159), the *Monocalyptus* suballiance is placed before the *Symphyomyrtus* suballiance, whereas *Monocalyptus* is placed after *Symphyomyrtus* in Pryor and Johnson, 1981: 504.

It appears that the species of subgenus *Glycaspis* (*Synglycaspis*) constitute the most ancient group in the genus because of the number of antennal rhinaria and their disposition (Eastop, 1958), and because of the gall-forming, flat and round-lerp forming habits of the species (Moore, 1961 *et seq.*).

Species of the subgenus *Glycaspis* (*Glycaspis*) construct the more advanced lerp shapes of round, oval, cloverleaf, square and rectangular, and bear progressively fewer antennal rhinaria, thus indicating that the group is of more recent origin than *Glycaspis* (*Synglycaspis*) in the evolutionary sequence of the genus.

The *Symphyomyrtus* suballiance may thus be considered of more recent origin than the *Monocalyptus* suballiance.

L. The species *G. atkinsoni* Moore (1984) colonizes EFAAA *E. similis* Maiden, and appears to be nearest to *G. violae* Moore (1970) which is known to occur on SUG:A *E. cambageana* Maiden and possibly SUP:V *E. melanophloia* F. Muell. *E. cambageana* is included in the 'box' group of eucalypts, and *E. melanophloia* in the 'ironbark' group (Chippendale, 1968).

E. similis is included in the 'subgenus' *Eudesmia* of Pryor and Johnson, 1971.

It is suggested that *E. similis* may have affinities with the 'box' and 'ironbark' groups of *Eucalyptus*.

HOST SPECIFICITY

Indications now suggest that certain species of *Glycaspis* are host-specific, and others may be termed Series-specific in the context of Pryor and Johnson's classification of the eucalypts (1971).

The above two categories of *Glycaspis* are listed, with the hosts alphabetical. Such lists are obviously incomplete and prone to revision because of limitations on past studies. They will provide a ready reference to most *Glycaspis* species hosts, thus facilitating identifications of *Glycaspis* species.

Lerp shapes are referred to in the lists by the following letters: G = galls; F = flat lerps; R = round; R-O = round to oval; CL = cloverleaf; S = square: RT = rectangular lerps.

Glycaspis spp. regarded as host-specific.

Subgenus *Synglycaspis*

amplificata	on	*E. acmenoides*	G
encystis	on	*agglomerata*	G
brunosa	on	*coccifera*	G
surculina	on	*conglomerata*	G
wallumaris	on	*conglomerata*	R
morgani	on	*diversifolia*	G
ecphymata	on	?*dives*	G
perthecata	on	*haemastoma*	G
icterica	on	*marginata*	R
munita	on	*nitida*	G
phreata	on	*oblonga*	F
belua	on	*pauciflora*	G
cyta	on	*pilularis*	G
seriata	on	*pilularis*	R
cyrtoma	on	*piperita*	G
planaria	on	*piperita*	F
longaeva	on	*pulchella*	G
nundlensis	on	*radiata*	F
immaceria	on	*rossii*	G
tagmata	on	*rodwayi*	F
obvelata	on	?*sieberi*	G
constricta	on	*stricta*	G
inclusa	on	*umbra*	G
orientalis	on	*umbra*	R

Subgenus *Glycaspis*

riguensis	on	*E. argophloia*	R-O
inusitata	on	*bakeri*	S, RT
rylstonensis	on	*blakelyi*	? R
clivosa	on	*brachyandra*	R
rubritincta	on	*brevifolia*	R
onychis	on	*brevifolia*	R
*blakei**	on	*camaldulensis*	CL
eremica	on	*camaldulensis*	CL
emphanes	on	*cambageana*	RT
subita	on	*cornuta*	R
deirada	on	*dundasii*	RT
montana	on	*dunnii*	R
exsertae	on	*exserta*	R
keremae	on	*exserta*	R-O
monita	on	*fasciculosa*	R-O
flavilabris	on	*goniocalyx*	R
caurina	on	*jensenii*	R
infucata	on	*leptopoda*	R
collina	on	*melanophloia*	R

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*one authentic record on *tereticornis*

neureta	on	*melliodora*	R-O
egregia	on	*moluccana*	R
mannifera	on	*moluccana*	R
praescopula	on	*orgadophila*	R-O
lacustris	on	*ovata*	R-O
pilata	on	*paniculata*	R
kurrajongensis	on	*paniculata*	R-O
mellialata	on	*paniculata*	R-O
permista	on	*paniculata*	R-O
suavis	on	*populnea*	R
imponens	on	*punctata*	R
operta	on	*raveretiana*	R
siliciflava	on	*robusta*	RT
xanthopepla	on	*seeana*	R
sudicola	on	*sideroxylon*	R-O
atkinsoni	on	*similis*	R
nancyana	on	*squamosa*	R
struicis	on	*tereticornis*	R
felicitaris	on	*tetraptera*	R
lucrosa	on	*tetrodonta*	R
wagaitjae	on	?*tetrodonta*	R
dobsoni	on	*viminalis*	R

Glycaspis spp. regarded as Series-specific

Subgenus *Synglycaspis*

aggregata	on 2 spp. in Series	Haemastominae	R
conserta	on 2 spp. in	Obliquae	R
cyanoreia	on 2 spp. in	Obliquae	R
endasa	on 2 spp. in	Piperitae	R
salebrosa	on 2 spp. in	Piperitae	R
temenicola	on 2 spp. in	Piperitae	R

Subgenus *Glycaspis*

wondjinae	on 3 spp. in Series	Albae	R
anota	on 2 spp. in	Miniatae	R
quornensis	on 2 spp. in	Moluccanae	R
aurosala	on 2 spp. in	Ochrophloiae	RT
whitei	on 2 spp. in	Polyanthemae	R
baileyi	on 3 spp. in	Salignae	R
ignea	on 3 spp. in	Salignae	R-O
granulata	on 3 spp. in	Salignae	RT
johnsoni	on 3 spp. in	Tereticornes	R
pratensis	on 2 spp. in	Tereticornes	R
minuscula	on 4 spp. in	Viminales	R

References

BLAKELY, W. F., 1955. — *A key to the eucalypts.* 2nd ed. Canberra: Forestry and Timber Bureau.
CHIPPENDALE, G. M., 1968. — *Eucalyptus buds and fruits.* Canberra: Forestry and Timber Bureau.

EASTOP, V. F., 1958. — Some neglected taxonomic characters of Psyllidae (Homoptera). *Ent. Mon. Mag.* 94 (1124): 18-19.

JOHNSON, L. A. S., 1972. — Evolution and classification in *Eucalyptus. Proc. Linn. Soc. N.S.W.* 97: 11-29.

——, 1976. — Problems of species and genera in *Eucalyptus* (Myrtaceae). *Plant Syst. Evol.* 125: 155-167.

MOORE, K. M., 1961a. — The significance of the *Glycaspis* species associations with their *Eucalyptus* spp. hosts; erection of a new subgenus and descriptions of thirty-eight new species of *Glycaspis. Proc. Linn. Soc. N.S.W.* 86: 128-167.

——, 1961b. — The biology and occurrence of *Glycaspis baileyi* Moore in New South Wales. *Proc. Linn. Soc. N.S.W.* 86: 185-200.

——, 1970. — A revision of the genus *Glycaspis* with descriptions of seventy-three new species. *Aust. Zoologist* 15: 248-342.

——, 1971. — The *Glycaspis* spp. — *Eucalyptus camaldulensis* associations. *J. Ent. Soc. Aust. (N.S.W.)* 7; 3-7.

——, 1975. — The *Glycaspis* spp. associated with *Eucalyptus camaldulensis. Proc. Linn. Soc. N.S.W.* 99: 122-128.

——, 1977. — Two new species of *Glycaspis* Taylor from Western Australia. *J. Aust. ent. Soc.* 16: 253-255.

——, 1978. — Further information on *Glycaspis* species associated with *Eucalyptus camaldulensis*, and other *Glycaspis* species. *J. Aust. ent. Soc.* 17: 257-260.

——, 1983. — New species and records of *Glycaspis* Taylor with phyletic groupings. *J. Aust. ent. Soc.* 22: 177-184.

——, 1984. — Two new species of *Glycaspis* from tropical Queensland, with notes on the genus. *Proc. Linn. Soc. N.S.W.* 107: 475-478.

——, 1985. — Four new species of *Glycaspis* Taylor (Homoptera: Spondyliaspididae) from some endangered species of *Eucalyptus. Proc. Linn. Soc. N.S.W.* 108: 71-78.

PRYOR, L. D., and JOHNSON, L. A. S., 1971. — *A classification of the eucalypts.* Canberra: Aust. National University.

——, and ——,, 1981. — *Eucalyptus*, the universal Australian. *In* A. KEAST, ed., *Ecological biogeography of Australia.* The Hague: W. Junk.

A new Species of *Glycaspis* (Homoptera: Spondyliaspididae) and some new Host Records

K. M. MOORE

MOORE, K. M. A new species of *Glycaspis* (Homoptera: Spondyliaspididae) and some new host records. *Proc. Linn. Soc. N.S.W.* 110 (1), (1987) 1988: 25-26.

A new species of *Glycaspis* Taylor from Collinsville, Queensland, is described and figured, and some new host associations and distributions are recorded.

K. M. Moore, Statue Bay, Yeppoon, Australia 4703; *manuscript received 3 June 1986, accepted for publication 18 February 1987.*

INTRODUCTION

With the description of this species, the subgenus *Glycaspis* of *Glycaspis* Taylor 1960 now consists of 88 species which are confined to the *Symphyomyrtus* suballiance of *Eucalyptus* L'Hérit. (Pryor and Johnson 1971).

DESCRIPTION AND NOTES

Glycaspis (Glycaspis) incomperta sp.n.

Figs 1-3

Types. Holotype ♂ on slide labelled Collinsville, Qld, 22 iii 1984, A. G. Webb, P052. Paratypes, 2 slides of single wholemount males with same label data, but P093 and P094 respectively.

Claspers and aedeagus as in Figs 1-3. Length of aedeagus 0.195-0.205mm (3 specimens).

All specimens are in the Australian National Insect Collection, CSIRO, Canberra.

Notes: The phyletic position of *G. incomperta* is in the *taylori* group, and appears to be nearest to *G. xanthopepla* Moore from which it differs in the following characters: the aedeagus is longer, with its distal end wider and more curved; posterior border of claspers more rounded, distal expansion of less area, the basal 'foot' of broader profile, fewer setae on external face.

The host of *G. xanthopepla* is *Eucalyptus seeana* Maiden the northern distribution of which reaches to about latitude 26°S. Collinsville is about 700km in a direct line from the nearest known occurrence of *E. seeana.*

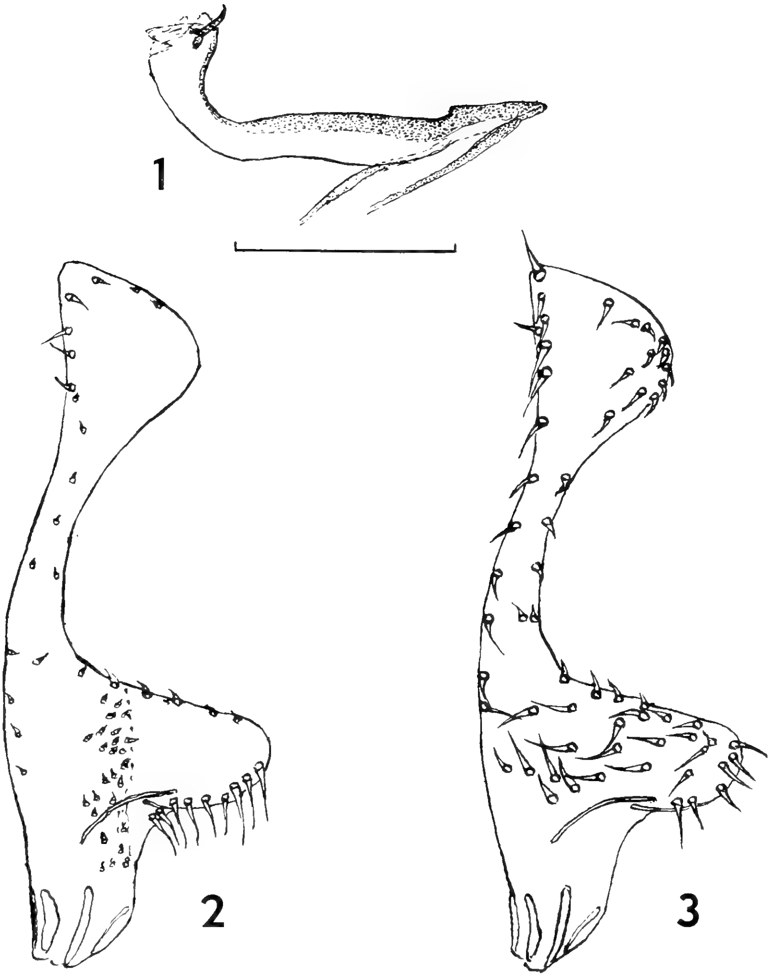
Etymology: Latin, *incomperta* = of which one has no information (on lerp shape or host).

NEW HOST RECORDS

Glycaspis (*Boreioglycaspis*) *devexa* Moore has now been found to colonize *Melaleuca dealbata* S. T. Blake, at 10km S Yeppoon.

G. (*B.*) *australiensis* Moore occurs on *Lophostemon* (= *Tristania*) *suaveolens* (Soland. ex Gaertn.) Wilson and Waterhouse, at Byfield State Forest, Yeppoon.

G. (*G.*) *brimblecombei* Moore colonizes *Eucalyptus mannifera* Mudie ssp. *maculosa* (R. T. Bak.) L. Johnson, and *E. brassiana* S. T. Blake grown from seed. Both hosts occurred at Canberra, A.C.T. (M. Carver, pers. comm., 1986).



Figs 1-3. Glycaspis incomperta sp.n. 1, aedeagus; 2, clasper, internal face; 3, clasper, external face. Posterior border of claspers on left. Scale line 0.1mm.

G. (*G.*) *minuscula* Moore previously known from *E. cinerea* F. Muell., *E. rubida* Deane and Maiden and *E. ?viminalis* Labill., also colonizes *E. pulverulenta* Sims at Cox's River on the Lithgow – Jenolan Road, N.S.W. (Collections made by K. G. Campbell, 1987).

References

PRYOR, L. D., and JOHNSON, L. A. S., 1971. – *A classification of the eucalypts.* Canberra: Aust. National University.

TAYLOR, K. L., 1960. – Additional information on the Australian genera of the family Psyllidae (Hemiptera: Homoptera). *Aust. J. Zool.* 8: 383-391.

First Report of Late Devonian Trilobites from eastern Australia

A. J. WRIGHT

WRIGHT, A. J. First report of Late Devonian trilobites from eastern Australia. *Proc. Linn. Soc. N.S.W.* 110 (1), (1987) 1988: 27-30.

Two generically indeterminate specimens of a phacopinid trilobite, of probable toIV — VI (late Famennian = late Late Devonian) age, are described and illustrated. From the Mandowa Mudstone near the township of Barraba, New England, N.S.W., these are the first recorded Late Devonian trilobites from eastern Australia.

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INTRODUCTION

Some years ago two trilobite specimens were collected by John Irving from mudstones outcropping adjacent to the Manilla River, east of Barraba, N.S.W. (Fig. 1). Both specimens lack any cephalic material (Fig. 2) but are clearly phacopid in nature, and are believed to be members of the subfamily Phacopinae as shown by the nature of the pygidium. They are recorded in this note as they are the only known Late Devonian trilobites from eastern Australia.

AGE AND STRATIGRAPHIC ASSIGNMENT

The locality (Fig. 1) falls within an area attributed by Chesnut *et al.* (1973) to the Late Devonian Mandowa Mudstone. Outcrops east of the town of Barraba (GR 278354) contain abundant *Leptophloeum australe* and rare shelly fossils including the trilobites recorded here, and may well have formed the original basis for the 'Barraba Series' (Benson, 1913). Mory (1982, fig. 4) gave an age of Early Carboniferous for the Mandowa

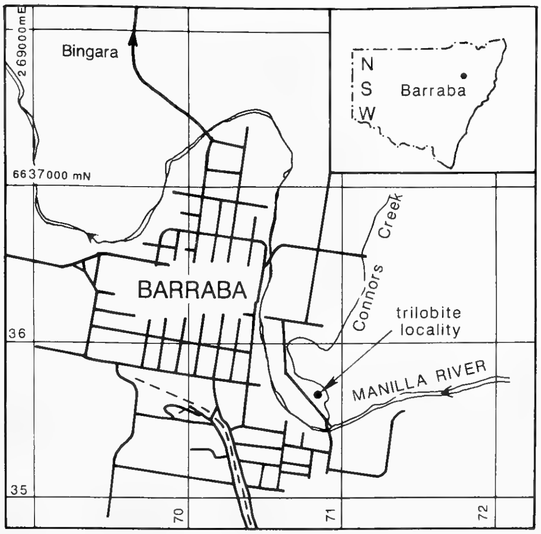
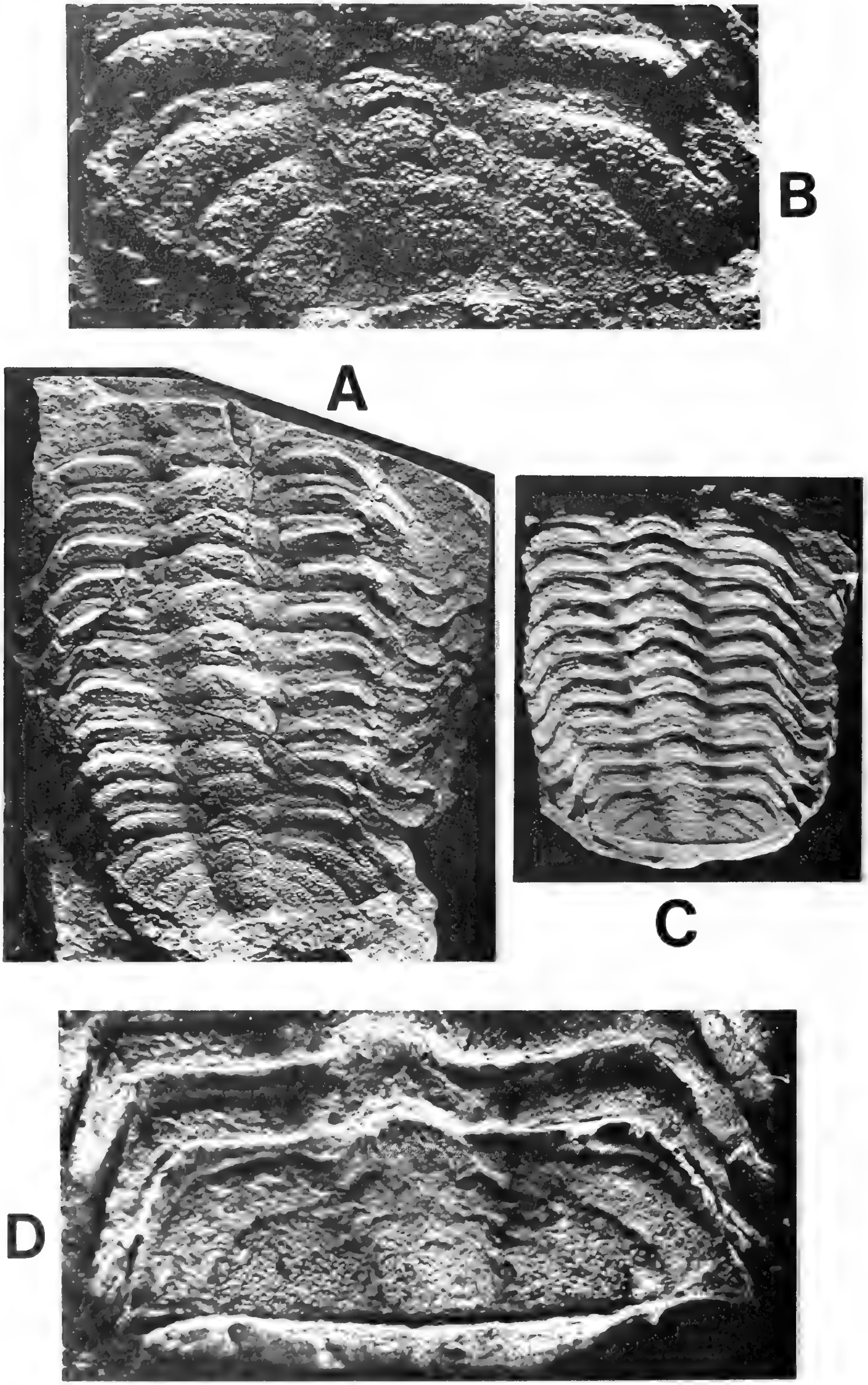


Fig. 1. Sketch map of Barraba township, showing approximate locality from which specimens were collected. Australian Map Grid, spacing 1km. Taken from Piedmont (9037-III-N) and Barraba (9037-III-S) 1:25,000 sheets.


B
A
C
D

Mudstone at Barraba, on the basis of the conodont *Siphonodella quadruplicata*. Dr Mory informs me (pers. comm., 1986) that his material was from outcrops west of the bridge on the northern side of the town, and that this locality appears to be considerably higher stratigraphically than the trilobite locality. Mory (1982) summarized conodont and ammonite data from the Mandowa Mudstone (incorporating data from Pickett, 1960; Jenkins, 1969, *in* Roberts, 1972), showing that fossils as old as the *Platyclymenia* — Stufe (toIV) of the Famennian (= upper part of Late Devonian) are present, and that conodonts from other localities suggest ages as young as Tn3 (Tournaisian = Early Carboniferous). The lycopod *Leptophloeum australe* occurs on the same rock as one of the trilobite specimens and is highly suggestive of a pre-Carboniferous age (Dr N. Morris, pers. comm., 1985).

Genera to which the trilobite specimens might belong on morphological grounds are: *Cryphops* (toI-IV); *Dianops* (toIV-VI); *Neophranops* (toI-III); or *Trimerocephalus* (toI-III). Given in parentheses are the ranges of genera as stated by Richter and Richter (1955, fig. 1) and Hahn and Hahn (1975) in terms of the German to (= *Stufe* or stage) terminology. (These subdivisions of the Late Devonian [see e.g. Roberts *et al.*, 1972, chart] are approximately toI = Frasnian and toII-VI = Famennian). These data indicate a Late Devonian age for the Mandowa Mudstone. However, on the basis of Mory's (1982) discussion, a maximum age of toIV is indicated for the Mandowa Mudstone. As only *Cryphops* and *Dianops* range above toIII, the specimens may be favoured to belong to one of these two genera or perhaps an undescribed genus. Identification to genus is not possible in the absence of cephalic material. Assignment of the material to the Phacopinae is indicated by the similarity of the pygidium to that illustrated by Struve *in* Moore (1959) for *Trimerocephalus* (although the material may not belong to that genus).

Both specimens have eleven thoracic segments with a granular prosopon which is also developed on the pygidium. The short, wide and flat pygidia exhibit three axial rings and a terminal piece, and three moderately curved pleural ribs with weak pleural furrows developed laterally. The posterior margin of the pygidium is gently convex, with a narrow marginal roll; the postero-lateral extremities are angular.

ACKNOWLEDGEMENTS

Thanks are due to Robert Jones (Australian Museum) and John Irving (amateur collector, Merrylands) for making this material available for study, and Dr Noreen Morris (University of Newcastle) for comments on the specimens of *Leptophloeum*. Research on Devonian faunas has been supported by the ARGS and the University of Wollongong.

References

BENSON, W. N., 1913. — The geology and petrology of the Great Serpentine Belt of New South Wales. Part i. Introduction. *Proc. Linn. Soc. N.S.W.* 38: 490-517.

CHESNUT, W. S., FLOOD, R. H., MCKELVEY, B. C., and CAMERON, R. G., 1983. — *Manilla 1:250,000 Geological Series, Sheet SH56-9 (1st Ed.).* New South Wales Geological Survey.

HAHN, G., and HAHN, R., 1975. — Die Trilobiten des Ober-Devon, Karbon und Perm. *In* KRÖMMELBEIN, K., (ed.), *Leitfossilien, begründet von Georg Gürich.* 2nd ed., 1. Berlin-Stuttgart: Gebrüder Borntraeger.

JENKINS, T. B. H., 1969. — Devonian of the Keepit Inlier. *In* PACKHAM, G. H., (ed.), The geology of New South Wales. *J. geol. Soc. Aust.* 16: 242-243.

——, 1972. — Tamworth Trough. *In* ROBERTS, J., *et al.* (1972): 480-481.

Fig. 2. Phacopinid, genus and species indeterminate. A, B, Australian Museum (AM) F65555. **A,** thorax and pygidium, x2.5; **B,** pygidium, x6. **C, D,** AM F72560. **C,** internal mould, thorax and pygidium, AM F72560b, x2; **D,** latex cast of external mould of pygidium, AM F72560a, x6.5. Both specimens from Mandowa Mudstone, near Barraba, New South Wales; probably to IV-VI (Late Famennian) in age.

MORY, A. H., 1982. — A review of Early Carboniferous stratigraphy and correlations in the northern Tamworth Belt, New South Wales. *Proc. Linn. Soc. N.S.W.* 105: 213-236.

PICKETT, J. W., 1960. — A clymeniid from the *Wocklumeria* Zone of New South Wales. *Palaeontology* 3: 237-241.

RICHTER, R., and RICHTER, E., 1955. — Oberdevonische Trilobiten Nachträge. 1. Trilobiten aus der *Prolobites*-Stufe III. 2. Phylogenie der oberdevonischen Phacopidae. *Senck. leth.* 36: 49-72.

ROBERTS, J., *et al.*, 1972. — Correlation of the Upper Devonian rocks of Australia. *J. geol. Soc. Aust.* 18: 467-490.

STRUVE, W., 1959. — Suborder Phacopina. *In* MOORE, R. C., (ed.) *Treatise on Invertebrate Paleontology* Part O. *Arthropoda*: 0461-495. Lawrence, Kansas: Geological Survey of America and University of Kansas Press.

Studies in Upside-down Flies (Diptera: Neurochaetidae) Part I. Systematics and Phylogeny

DAVID K. MCALPINE

MCALPINE, D. K. Studies in upside-down flies (Diptera: Neurochaetidae). Part I. Systematics and phylogeny. *Proc. Linn. Soc. N.S.W.* 110 (1), (1987) 1988: 31-58.

Neurocytta and *Neurotexis* are described as new subgenera of *Neurochaeta*. *Neurochaeta* (*Neurochaeta*) *magnifica* (Papua New Guinea), *Neurochaeta* (*Neurochaeta*) *capilo* and *Neurochaeta* (*Neurochaeta*) *parviceps* n.spp. (West Malaysia) are described. The genus *Nothoasteia* is transferred from Asteiidae to Neurochaetidae and *Nothoasteia clausa* n.sp. (Western Australia) is described. The ground-plan characters for the Neurochaetidae are given in the light of the newly included taxa, and variation in the structure of the arista, the prosternum, the scutellum, and the postnotum is examined. Phylogeny within the family is discussed. Keys to genera, subgenera, and species are given.

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manuscript received 21 May 1986, accepted for publication 22 July 1987.

INTRODUCTION

Since the family Neurochaetidae was established for the living *Neurochaeta* McAlpine and the Baltic amber fossil *Anthoclusia* Hennig (McAlpine, 1978), more material and information have become available. Field studies of the Australian species have been carried out (Shaw, Cantrell, and Houston, 1982; Shaw and Cantrell, 1983a, 1983b; author's observations). Woodley (1982) has described two Oriental species of *Neurochaeta* and made a phylogenetic analysis for the genus. The author's work (with the help of K. C. Khoo) has brought to light additional species from Malaysia together with information on apparent host plants, and J. W. Ismay has discovered a species in Papua New Guinea. A further specimen of the little known genus *Nothoasteia* Malloch has become available, thanks to A. C. Postle and B. Cantrell, and evidence has been obtained indicating that it should be transferred from the Asteiidae to the Neurochaetidae.

The number of recognized living species of the family now stands at 10, while there are 2 fossil species described by Hennig (1965, 1969).

The morphological terminology here used has been largely outlined by McAlpine (1973a) or is given by Colless and McAlpine (1970).

While the identity of the protandrial sternites (those of abdominal segments 6-8) in the Schizophora is now agreed upon by a number of workers (e.g. Crampton, 1942; Griffiths, 1972), the identity of certain other postabdominal structures remains controversial. I am quite sceptical about many attempts to homologize structures over a wide spectrum of the order Diptera and even more so with attempts at homology between Diptera and other orders. I use the terms epandrium, hypandrium, surstylus, and gonite to designate structures readily identified by their positions, but because of the great variability they exhibit, I have no confidence that the two latter terms are consistently applied to homologous structures, and this applies also to the popular Comstock-Needham nomenclature for wing veins.

FAMILY NEUROCHAETIDAE

The addition of the genus *Nothoasteia* makes my previous characterization of the family (McAlpine, 1978) inadequate. I do not herein give a revised characterization because the morphology of *Anthoclusia* and *Nothoasteia* is still incompletely known, but the characters given below for *Nothoasteia* may be taken as an extension of the family characters. Alternatively, a statement of the groundplan characters for Neurochaetidae is difficult, because the precise phylogenetic position of *Nothoasteia* is unclear, on account of its highly autapomorphic and incompletely known morphology. It is therefore not known to what extent the groundplan characters for *Anthoclusia* + *Neurochaeta* (largely typified by *Anthoclusia*), are also those for *Nothoasteia* + *Anthoclusia* + *Neurochaeta*. The following characterization is therefore provisional.

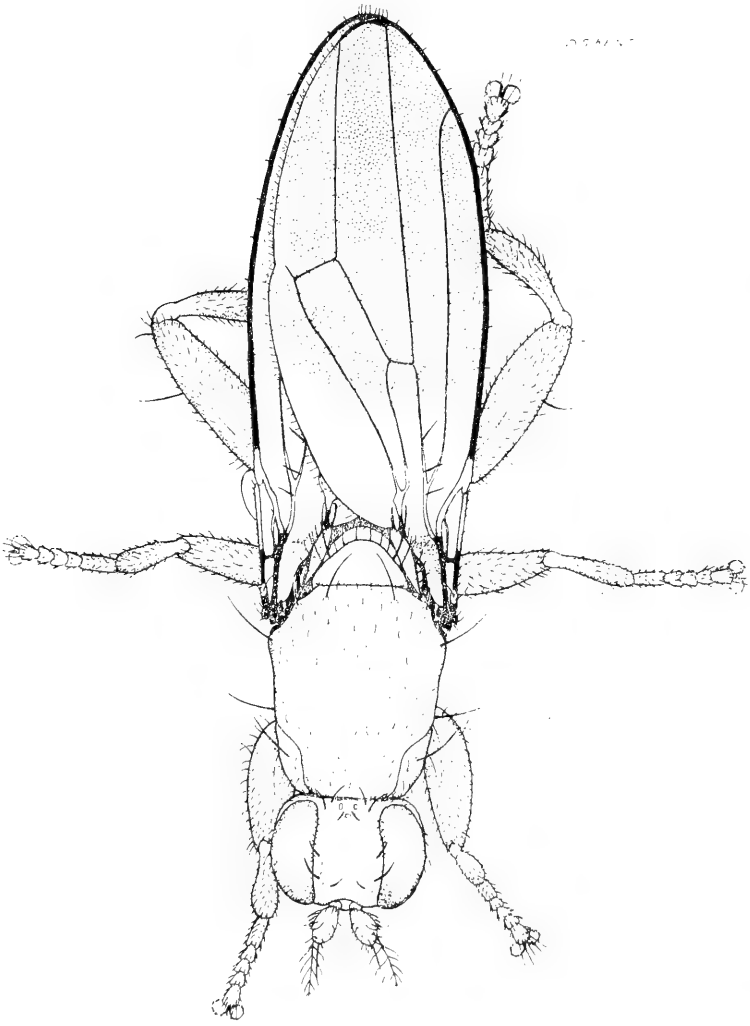


Fig. 1. Neurochaeta inversa (based on a photograph from life).

Groundplan characters of Neurochaetidae

General characters as for superfamily Asteioidea (McAlpine, 1978); postvertical bristles parallel to slightly divergent, posteriorly directed; vibrissa and peristomal bristles present; antennal segment 2 cap-like, with dorsal slit; segment 3 deflexed;

labella of proboscis broad; postnotal region elevated; with relatively small subscutellum; prosternal plate (basisternum) narrow, joined to angular median prominence of the well defined furcasternum; the following thoracic bristles present: humeral, 2 notopleural, 2 dorsocentral, supra-alar, postalar, 2 unequal scutellars, 2 upper posterior sternopleurals; the following bristles absent: presutural, posterior intra-alar, propleural; hind leg longer than other legs; mid coxae approximated; mid femur significantly shorter than hind femur and more slender than fore femur; costa broken only at end of subcosta; subcosta indistinct distally; second basal, discal, and anal cells complete; vein 6 sclerotized beyond anal cell but not reaching margin; alula distinct; preabdominal sternites broad; tergite 6 of ♂ unreduced; cerci distinct and separate in both sexes.

Morphology of the arista

I have previously discussed antennal structure in the Asteioidea (McAlpine, 1978; 1983). The arista of *Neurochaeta inversa* is of a somewhat reduced type: segment 4 is not discernible, segment 5 is very short and annular, and segment 6 has long branches, some of the dorsal ones arising close to its base. This is not in agreement with the arista of *Anthoclusia gephyrea* as figured by Hennig (1965: fig. 247B), which appears to have a somewhat elongate, cylindrical segment 5, and segment 6 with branching less developed at its base. On the whole dry specimen, the arista of *Nothoasteia clausa* appears to have segment 5 almost as short as in *Neurochaeta inversa*, but segment 6 has no major branches, only short hairs. A more thorough study of the morphology of the arista in Neurochaetidae will be necessary to evaluate its use in determining phylogeny.

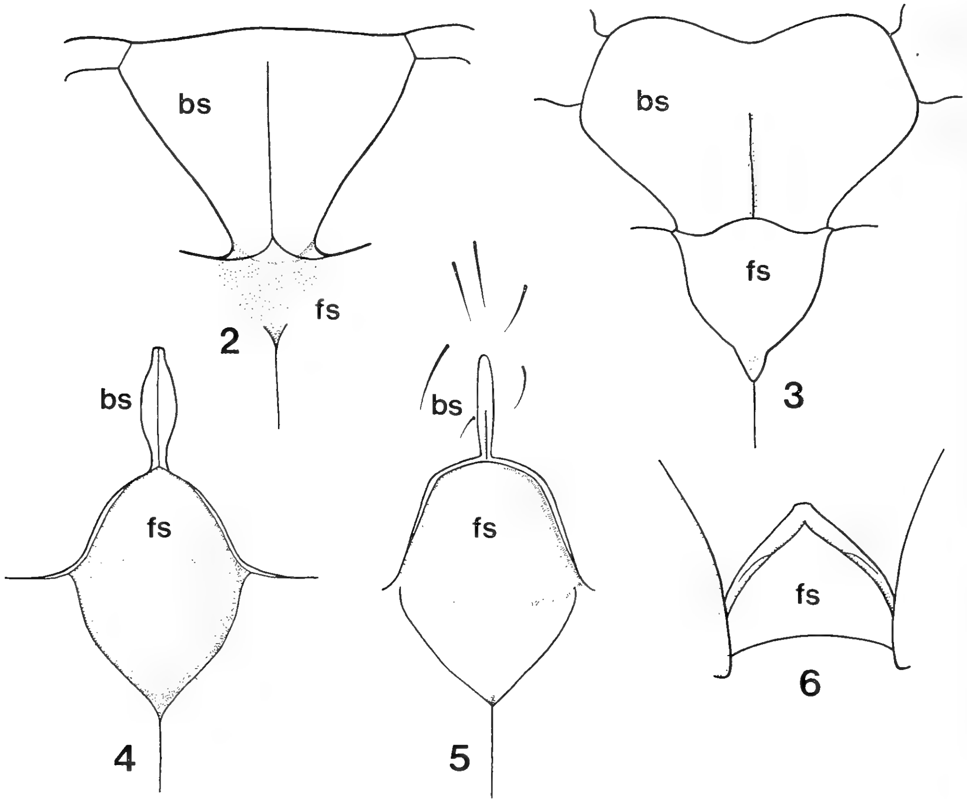
Morphology of the prosternum

As the prosternal characters are of both taxonomic and adaptational significance, their variation is here described.

The prosternum of the Neurochaetidae is characterized by reduction, through narrowing, of the basisternum (the sternal plate which is well developed and distinct in most higher Diptera); and the angular anterior production of the furcasternum, to the apex of which the basisternum is usually joined.

A greater development of prosternal structures is seen in *Cyamops* (Fig. 3), a genus of the apparently related family Periscelididae. The furcasternum, often invisibly fused with the sternopleura (katepisterna) in other Schizophora, is defined by a V-shaped suture and has a distinct furcal pit in its posterior angle. The very broad basisternum is joined posteriorly to the furcasternum and anterolaterally to precoxal bridges of the propleura. The obvious suture on the precoxal bridge of each side possibly indicates that this bridge is an apomorphic development within the family Periscelididae, as it is absent in *Scutops* and *Periscelis*. The periscelidid genus *Stenomicra* (Fig. 2) has a somewhat similar prosternum to that of *Cyamops*, but the sutures defining the fucasternum from the sternopleura are not visible in the examples studied, though the cuticle is sufficiently transparent to show any sutures. All these forms have a distinct median line or groove on the sternopleura indicating the internal ridge which extends posteriorly from the furcal pit.

Neurochaeta inversa (Fig. 4) retains a large, convex, well defined furcasternum, but the furcal pit is evident only as the angular junction of the grooves along the suture delimiting the furcasternum from the sternopleura. The basisternum is much reduced in size, but not linear, with a marked median groove. In some individuals (more frequently in ones from northern populations) there is a fine hair in the sternal membrane on each side of the basisternum.



Figs 2-6. Prosterna of periscelidids and neurochaetids. 2. *Stenomicra* sp. (Mount Wilson, N.S.W.). 3. *Cyamops dayi* Khoo. 4. *Neurochaeta inversa.* 5. *Neurochaeta parviceps.* 6. *Nothoasteia clausa* (showing margin of fore coxa at each side). bs = basisternum. fs = furcasternum.

In *Neurochaeta parviceps* (Fig. 5) and closely related species the basisternum is reduced to a narrow-linear sclerite and the hairs in the adjacent membrane are well developed.

In *Neurochaeta magnifica* the basisternum is very broad, with several setulae (Fig. 23). In accordance with the evidence that (a) the reduced, narrowed prosternum is the normal condition of all subgenera of *Neurochaeta*, and (b) *N. magnifica* is derived from among the more apomorphic types of the subgenus *Neurochaeta*, I regard this condition as a secondary sclerotization which I shall later relate to other peculiar features of the prothoracic region in this species.

Nothoasteia clausa shows the most remarkable degree of reduction of prosternal structure (Fig. 6), but this appears to be an extreme development of the condition seen in *Neurochaeta*. No trace of the basisternum remains. The furcasternum is angular anteriorly as in *Neurochaeta*, with relatively broad raised margin; posteriorly it is delimited by a simple transverse line and is without the sternal pit. There is no median suture extending posteriorly from this transverse suture (hence no internal median ridge), the sternopleura of each side being indistinguishably fused except towards their posterior extremities.

The prosternum of *Anthoclusia* is not known in detail. Hennig (1969) merely states for *A. remotinervis*, that the prosternum is apparently not connected to the propleuron by a precoxal bridge, and I found it difficult to interpret the prosternal structure during my brief examination of this specimen.

Morphology of the scutellum and postnotum

The scutellar region and scutellar chaetotaxy of *Anthoclusia gephyrea* very probably represent the most plesiomorphic conditions among known neurochaetids. This statement is made because *A. gephyrea* has the thorax at an evolutionary stage which precedes marked dorsoventral compression, because the scutellum and postnotal region resemble those of the periscelidid genera *Cyamops* (Fig. 7) and *Periscelis* (the family Periscelididae being the apparent sister-group of Neurochaetidae if it is monophyletic), because the general morphology and time level of *A. gephyrea* indicate that it is a very plesiomorphic neurochaetid; and because the variations in scutellar chaetotaxy in the genus *Neurochaeta* are readily explained as simple or serial derivatives from it.

The scutellum of *A. gephyrea* (Hennig, 1965: fig. 248) is subtriangular with a broadly rounded apex; it appears to be somewhat flattened on the dorsal surface and quite thick at the free margins. There is a small lateral pair of bristles situated some distance behind the scutellar suture, and a large subapical pair of bristles. Because of variation in the position of the latter pair, they are hereafter referred to as the major pair of scutellar bristles. It is uncertain if their suberect position shown in Hennig's figure is natural or not.

The scutellum of *Anthoclusia remotinervis* differs from the above in loss of the lateral pair of bristles (Hennig, 1969).

In the genus *Neurochaeta* the scutellum has become markedly shortened and more or less depressed relative to that of *Anthoclusia gephyrea*, but otherwise the structure of the scutellum exhibits diverse levels of specialization among the species.

In *Neurochaeta prisca* (McAlpine, 1978: fig. 11) the outline of the scutellum retains something of the plesiomorphic triangular shape despite the shortening, and the major bristles remain close together near the apex. Each lateral bristle is replaced by a series of setulae, an apomorphy unique in the family.

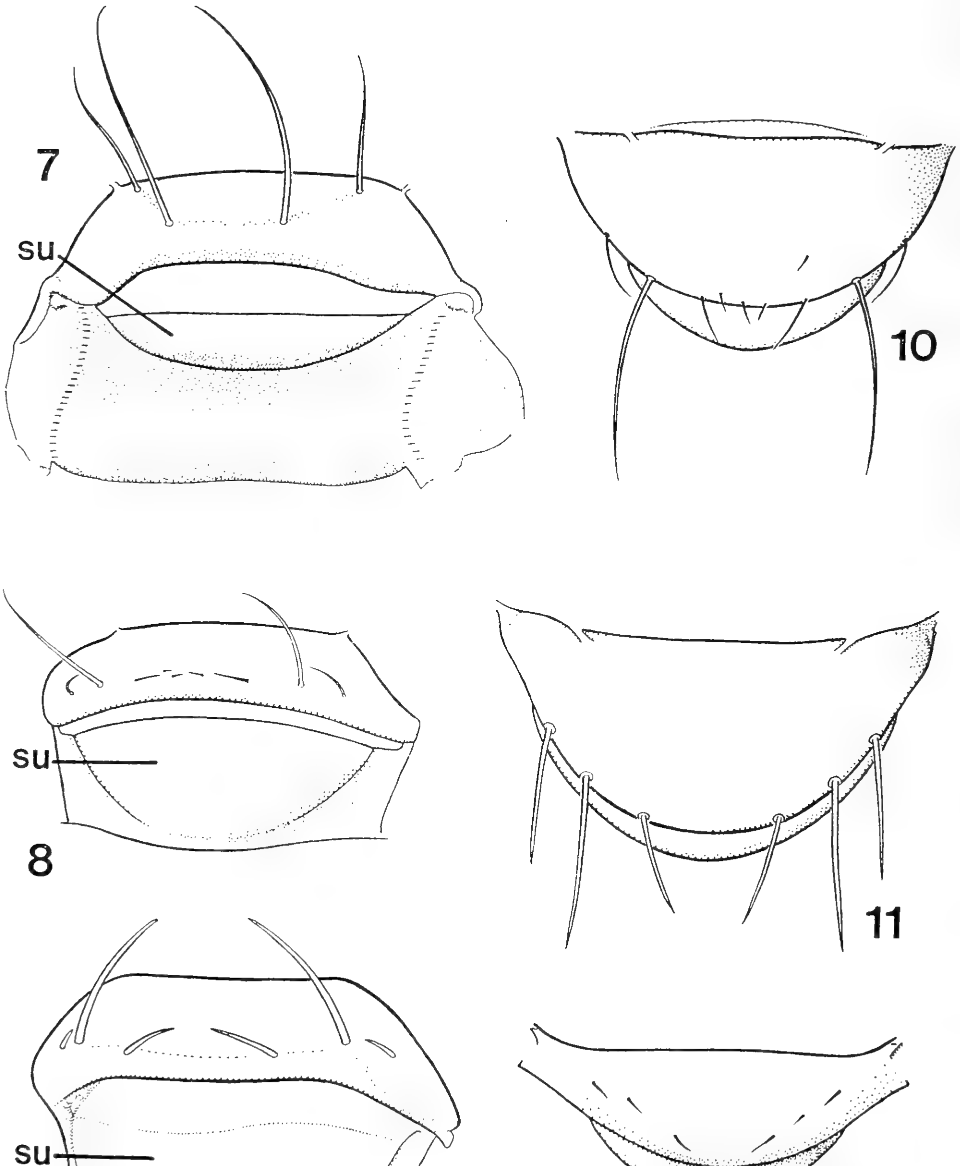
The remainder of the species of *Neurochaeta* (subgenera *Neurotexis* and *Neurochaeta*) have the scutellum usually with evenly rounded outline (tending towards a semicircle) and the major bristles are markedly laterally displaced. *Neurochaeta* (*Neurotexis*) *stuckenbergi* has retained the scutellum at this level of specialization (McAlpine, 1978: fig. 12).

The subgenus *Neurochaeta* is characterized by acquisition of additional bristles or setulae between the major pair, on or near the posterior margin. These I term the posterior scutellar bristles for descriptive purposes. The tendency towards a more erect position of the bristles is apparent throughout the subgenus, but the variation, with retention of symmetry, seen in dried material of *Neurochaeta capilo* and, especially, *N. inversa* seems to indicate much mobility of the major pair in life.

In *N. capilo* (Fig. 10) there is one pair of short convergent bristles near the apex of the scutellum and few, often asymmetrically placed setulae near them. This somewhat irregular arrangement may represent an approximation to an early stage of evolution of these posterior macrotrichia.

In *N. inversa* (McAlpine, 1978: fig. 16) the posterior macrotrichia are represented by a regular linear series of rather short bristles along the posterior margin of the scutellum, in two to four (usually three) pairs. In *N. magnifica* the arrangement of the posterior bristles is similar, but there are four to seven pairs.

The scutellum in the *parviceps* group (Figs 9, 11) has the major bristles shorter and more consistently erect (or less posteriorly inclined) than those of *N. capilo* and *N. inversa*,



Figs 7-12. Scutella and postnota of periscelidids and neurochaetids. 7. *Cyamops dayi* (posterior aspect). 8. *Neurochaeta capilo* (posterior). 9. *Neurochaeta macalpinei* (posterior). 10. *Neurochaeta capilo* (dorsal). 11. *Neurochaeta parviceps* (dorsal). 12. *Nothoasteia clausa* (dorsal). su = subscutellum. In Fig. 11 bristles shown as if extended horizontally.

and the posterior bristles represented by one pair, each of which is closer to the major bristle than to the other posterior bristle. This arrangement of the posterior bristles may have been evolved through condensation of the linear series seen in *N. inversa*, or, alternatively, it may have been attained directly from the less ordered configuration of *N. capilo.* In the latter case, *N. inversa* and the *parviceps* group have acquired independent apomorphic conditions of the posterior bristles. *Neurochaeta parviceps* has all three pairs of scutellar bristles more similar in length than in other species of the group. (In Fig. 11 the suberect bristles of the major pair have been drawn as if in a horizontal plane.) *N. sabroskyi* probably has the scutellar bristles similar to those of *N. parviceps*, but in the unique holotype only the lateral bristles are preserved. *N. macalpinei* has many of the body bristles shortened as an autapomorphy, but it is not clear precisely how this general process has affected the scutellar bristles. In contrast to *N. parviceps*, the major bristle in *N. macalpinei* (Fig. 9) is about twice as long as the lateral bristle or the posterior bristle, but the major bristle is only slightly shorter than that of *N. parviceps* relative to the distance between the bases of the major bristles. This size differentiation may be the retention of a plesiomorphic condition, as perhaps is that of *N. capilo*, or a late apomorphy derived from the condition seen in *N. parviceps*, out-group comparison (for the *parviceps* group) suggesting the former. In *N. macalpinei* the major bristles are strongly convergent and their backward inclination is minimal.

The scutellum of *Nothoasteia clausa* (Fig. 12) has some points of resemblance to that of the *parviceps* group of *Neurochaeta*; in particular it is flat, with rounded posterior margin but is even shorter; there are 3 pairs of bristles though these are all much shorter than in the *parviceps* group and directed posteromedially. On its appearance, without reference to other facts, the scutellum might be considered to be derived from that of the *parviceps* group, but, as shown below this is negated by other evidence.

The postnotal structure of the periscelidid genus *Cyamops* (Fig. 7) is taken as representing a generalized condition near that of the groundplan of the Periscelididae-Neurochaetidae (and perhaps of the Asteioidea), which preceded dorsoventral compression. Immediately below the free posterior margin of the scutellum there is a narrow transverse zone of membranous cuticle, the subscutellar membrane. The median sclerotized part of the postnotum (mediotergite), lying below the scutellum, consists of two distinct convex zones, the smaller upper subscutellum and the lower postscutellum, which slopes posteriorly to the first abdominal tergite.

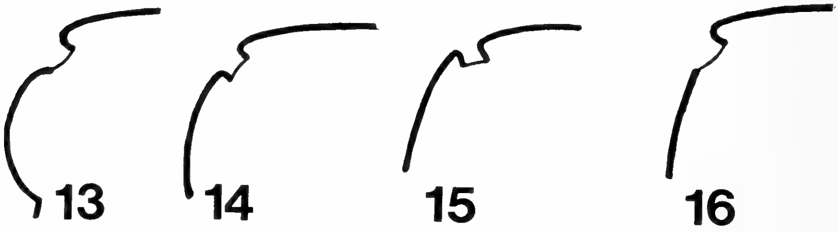
Postnotal structure in *Anthoclusia gephyrea* appears not to differ from the above condition so far as I can discern from the imperfect detail in the illustration by Hennig (1965: fig. 248). In particular the posterior margin of the scutellum remains quite deep and the subscutellum is markedly smaller than the well developed postscutellum. Other neurochaetids all have the postnotal region reduced in depth, apparently as a result of dorsoventral compression of the thorax.

Unfortunately I no longer have study material of *Neurochaeta prisca* for detailed comparison. My previously recorded observations (McAlpine, 1978: 282) indicate a significant reduction in depth of the postnotum without its acquiring a prominently convex condition. This perhaps indicates that much of its remaining surface consists of postscutellum rather than subscutellum, in contrast to the other species of the genus *Neurochaeta*.

Interpretation of postnotal structure in the subgenus *Neurochaeta* is aided by reference to its most plesiomorphic species, *N. capilo* (Fig. 8), but the structure of the latter has evolved far beyond the apparent neurochaetid groundplan and no known neurochaetid represents a clearly intermediate stage.

The morphologically diverse periscelidid genus *Stenomicra* shows a range of postnotal structure which parallels some of the probable evolutionary stages of neurochaetids between the groundplan condition and that of *N. capilo.* In *Stenomicra* sp. (West Malaysia, Australian Museum, a remarkably plesiomorphic representative of the genus), the condition is rather similar to that of *Cyamops* as described above, but the subscutellum has become enlarged at the expense of the postscutellum. In other species of *Stenomicra* (subgenera *Podocera* and *Stenomicra*) the subscutellum becomes very convexly prominent and increases further in depth. It approaches the first abdominal tergite on the median line in extreme cases, thus almost dividing the postscutellum in two.

Neurochaeta capilo has the postnotal region (Fig. 8) somewhat resembling the condition described for the more apomorphic species of *Stenomicra*, but there has been a decrease in depth and the subscutellum is broader, almost as wide as the postscutellum, strongly convex, with narrowly acute lateral extremities. The visible demarcation between subscutellum and postcutellum is not sharp, partly from the dense clothing of silvery pruinescence, but it appears that the subscutellum is only narrowly separated from the first abdominal tergite on the median line by the medially narrowed postscutellum. The upper margin of the subscutellum, where it meets the subscutellar membrane, is incurved in conformity with the general convexity of the surface, but is not abruptly inflexed (Fig. 13).



Figs 13-16. Diagrams of scutellar and postnotal structures in *Neurochaeta* in vertical longitudinal section, scutellum at top, postnotum at left, subscutellar membrane indicated by thin line. 13. *N. capilo.* 14. *N. inversa.* 15. *N. magnifica.* 16. *N. parviceps.*

The *inversa*, *magnifica* and *parviceps* groups of *Neurochaeta* have the subscutellum both deeper and broader than in *N. capilo* and the postscutellum thus reduced to two small lateral pieces (Fig. 9).

In the *inversa* and *magnifica* groups, but not in the *parviceps* group, the upper margin of the subscutellum is abruptly inflexed, so that there is a trough between the scutellum and subscutellum, the floor of which is formed by the subscutellar membrane (Figs 14, 15).

I no longer have access to material of *Neurochaeta stuckenbergi.* Clearly this species has a strongly convex postnotal region largely developed from the postscutellum but other details were not recorded.

Again there is resemblance in postnotal structure between *Nothoasteia* and the most apomorphic species of *Neurochaeta. Nothoasteia clausa* has the subscutellum very convex and shallow, but almost entirely filling the area between the scutellum and the base of the abdomen, the postscutellum being reduced to two small lateral plates. No subscutellar membrane is visible in the only specimen, the sclerotized subscutellum being appressed to the ventral part of the scutellum.

Hardy (1950) has recorded what he termed 'the articulating scutellum' in a number of brachycerous Diptera, including several of the Schizophora, where the condition is apparently of wide occurrence. Examination of series of dried specimens of *Neurochaeta inversa* and *N. parviceps* indicates that movement occurs between the scutellum and subscutellum. The subscutellar membrane becomes infolded when these parts are appressed, and the margin of the scutellum becomes partly enveloped by the upper margin of the subscutellum. In the available specimen of *Nothoasteia clausa* the upper margin of the subscutellum passes beneath the scutellum, but does not envelop it. The relations of these parts are shown diagrammatically in Figs 13-16.

Phylogeny

The apparent phylogenetic lines in the family, leaving out of consideration *Nothoasteia* and the new species of *Neurochaeta* here described, are given by Woodley (1982). It remains for these taxa to be added to Woodley's system.

At the time of Woodley's work it appeared that the apomorphic condition of character 3 (posterior cubital or anal cell reduced or absent) was a groundplan state for *Neurochaeta stuckenbergi* + the *N. inversa* group (i.e. subgenera *Neurotexis* and *Neurochaeta* in the present work). The newly discovered species *N. capilo* is undoubtedly a member of the latter group of this pair but has a complete anal cell and sclerotized vein 6 beyond it. It seems, then, that reduction of the anal cell (and vein 6) has taken place independently in these two subgenera. I believe evidence for sister-group relationship between subgenera *Neurotexis* and *Neurochaeta* is confirmed by the following apomorphic characters in relation to the subgenus *Neurocytta* (including *N. prisca*): costa with subcostal break obliquely incised to produce a lobe; subscutellum deep and convexly prominent; major (primarily apical) pair of scutellar bristles displaced laterally; only one upper posterior sternopleural bristle present.

The revised set of distinctive apomorphic characters for the subgenus *Neurochaeta* (the '*N. inversa* species group' of Woodley, expanded to include new species) is as follows: fronto-orbital bristles reduced to 3 pairs; postvertical bristles lost; a series of postgenal bristles present; suborbital bristle present (below lowest point of eye, see Figs 18, 26); second (from rear) dorsocentral bristle reduced and approximated to prescutellar dorsocentral, or lost; scutellum with at least one pair of posterior marginal bristles or hairs between major pair; sternopleuron anteriorly with group of strong hairs or bristles; macrotrichia on radial sector developed as about 3 strong bristles; second basal cell confluent with first basal cell; ♂: surstylus detached from margin of protandrium.

The subgenus *Neurochaeta* includes the *capilo*, *inversa*, *magnifica*, and *parviceps* groups, as newly defined here.

The position of *Neurochaeta capilo* as a sister group to the remainder of subgenus *Neurochaeta* (*inversa* group sensu Woodley) is evidenced by its having the following plesiomorphic characters relative to those uniformly present in the rest of the subgenus: thorax not strongly depressed; 2 dorsocentral bristles present; anterior sternopleural bristles not differentiated; mid coxae almost contiguous; anal cell closed by distinct, curved anal crossvein; vein 6 developed beyond anal cell; sternite 8 of male large; cercus of ♀ small, not plate-like. For these reasons I place *N. capilo* as the only known species of the *capilo* group.

The apomorphic characters differentiating the *parviceps* group (*N. sabroskyi*, *N. parviceps*, and *N. macalpinei*) are: suborbital bristle curved downwards; prelabrum much reduced; palpus very short; propleuron without distinct callus; prosternum narrow-linear; metasternum extensively setulose; mid coxae separated by at least width of each coxa; mid femur with ventral comb of weak bristles; vein 5 not extending beyond discal cell. The monotypic *inversa* group lacks the above characters, but has apparently few

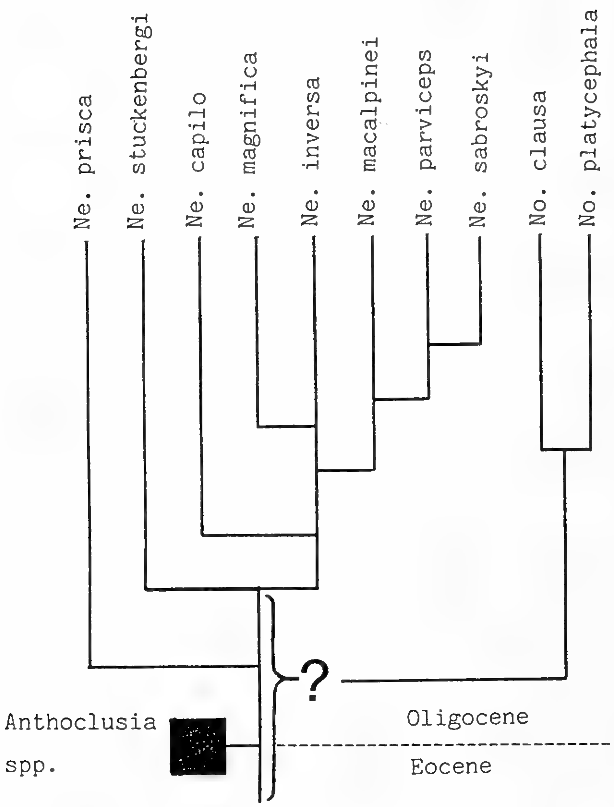


Fig. 17. Dendrogram showing apparent interrelationships of neurochaetid taxa.

apomorphic characters not shared with the *parviceps* group, viz.: posterior scutellar bristles forming a regular transverse series; dorsal margin of subscutellum inflexed; sternite 8 of ♂ absent; and (probably) propleural callus enlarged. The group is, however, intermediate between the *capilo* group and the *parviceps* group in several characters, viz. degree of development of anterior sternopleural bristles; incipient setulosity of metasternum; degree of separation of mid coxae; length of tarsal claws; position of anterior (incurved) fronto-orbital bristle.

The *magnifica* group (also monotypic) has an extraordinary array of apomorphic characters, including all those given for the *inversa* group except loss of ♂ sternite 8, some of those given for the *parviceps* group (viz. metasternum extensively setulose; mid coxae separated by at least width of each coxa), and numerous apparently autapomorphic characters (e.g. head depressed; inner vertical bristle absent; anterior notopleural bristle displaced dorsally; hypopleuron setulose; prosternum very broad; hind femur much longer than thorax; costal armature simplified). The apparent conflict in phylogenetic evidence from variously shared apomorphic characters and the phenetic remoteness from other species of subgenus *Neurochaeta* complicate the problem of the immediate relationships of *N. magnifica*. Careful consideration leads me to the conclusion that those characters shared with the *inversa* group are most likely to be true synapomorphies (although the first two are present in an exaggerated form in *N. magnifica*), while the characters shared with the *parviceps* group are convergent. The broadly exposed, setulose metasternum and widely separated mid coxae are associated with a broadening and flattening of the thorax in a number of separately derived dipterous types (e.g. *Coelopa*, *Orygma*, the pupiparous flies). That a broadly flattened thorax has been achieved to some extent independently in the *parviceps* and *magnifica* groups is evidenced particularly in the position of the fore coxae and their relation to the pleura. In the face of contrary evidence, then, the shared apomorphic characters in the two groups do not carry conviction as true synapomorphies. I therefore postulate a sister-group relationship between the *inversa* and *magnifica* groups. This is in accordance with geographic distribution, as these are the only groups of *Neurochaeta* in the Australian (Australasian) Region.

The phylogenetic position of the genus *Nothoasteia* in relation to other neurochaetids is difficult to determine. The genus was originally placed in the family Asteiidae by Malloch, 1936, with considerable doubt. The following is a list of those characters for *Nothoasteia*, which have influenced me in transferring the genus from the Asteiidae to the Neurochaetidae.

1. Antennal segment 2 cap-like, with dorsal slit (not cap like, with dorsal part of distal margin slightly sinuate only, in Asteiidae).
2. Upper occiput without trace of deep, broad concavity characteristic of Asteiidae (including *Succinasteia* and *Leiomyza*).
3. Prothoracic basisternum greatly reduced in a broad, membranous intercoxal field; furcasternum with acute anterior lobe. These characters are peculiar to the Neurochaetidae among the Asteioidea (see further discussion above). The Asteiidae have the prosternum broad, sometimes little sclerotized, joined to the almost straight, transverse anterior margin of apparent mesosternum.
4. Metasternum separated from hypopleuron on each side by membrane of hind coxal cavity (narrowly joined to hypopleuron in *Neurochaeta*, usually very broadly joined in Asteiidae).
5. Fore coxa short (generally relatively long and slender in Asteiidae).
6. Mid coxae very short, separated (mid coxae contiguous and relatively prominent in Asteiidae).
7. Hind coxal cavities directed posteriorly to posterolaterally (directed ventrally in Asteiidae).
8. Hind legs (particularly hind femora) enlarged; mid legs reduced in size. This is a slight extension of the highly characteristic leg proportions seen in other neurochaetids. (Asteiidae never have such disparity in leg size.)
9. Vein 6 more complete than in any known asteiid (including *Succinasteia*).
10. Abdominal sternites broader than in any asteiid known to me (including *Succinasteia*), despite the more slender abdomen. The broadened sternites are particularly characteristic of the Neurochaetidae.

In making the above comparison I have referred to Hennig's (1969) detailed description of the Baltic amber fossil *Succinasteia carpenteri*, which could represent the stem group from which all recent Asteiidae were derived. I have also examined *Bryania bipunctata* Aldrich and an undetermined asteiid from Papua New Guinea, both of which have, like *Nothoasteia*, a somewhat depressed body form. They do not, however, show significant resemblance to *Nothoastia* in other characters.

Nothoasteia resembles the Asteiidae (or at least some of its species) in its small size, reduced chaetotaxy, and reduction in wing venation, all characters where convergence is most apt to occur, the two latter states often accompanying size reduction in various acalyptrate groups. The absence of a costal break, shared by *Nothoasteia* and Asteiidae, has been considered a plesiomorphic character by Hennig (1958), but, as Griffiths (1972) has pointed out, it is likely to be an apomorphic acquisition in the groundplan of the Asteiidae. It appears to represent an independent autapomorphy in *Nothoasteia*.

It has been suggested, without reference to specimens, that *Nothoasteia* may belong in the family Anthomyzidae, but I do not consider that this is a reasonable theory. I know of no significant apomorphies shared between it and the anthomyzids, and *Nothoasteia* differs in characters of antenna, prosternum, leg proportions, and mid coxae, much as it differs from Asteiidae. Possibly, Anthomyzidae and Asteiidae are more closely related to each other than either is to *Nothoasteia* and the Neurochaetidae.

Within the Neurochaetidae, *Nothoasteia* resembles *Anthoclusia* more than other known forms in the development of antennal segment 2. This would appear to exclude it from immediate relationship with subgenera *Neurotexis* and *Neurochaeta* which share the enlarged, hood-like segment 2, probably as a synapomorphy. Unfortunately the antenna of subgenus *Neurocytta*, evidently a sister group to the rest of genus *Neurochaeta*, is unknown. The probably plesiomorphic approximation of the apical scutellar bristles in *Nothoasteia* seems to confirm its exclusion from this *Neurotexis-Neurochaeta* complex. Possibly the more cylindrical abdomen, excludes *Nothoasteia* from close relationship with the whole genus *Neurochaeta*, but this character needs further study. The confluence of the second basal and discal cells in both *Nothoasteia* and subgenus *Neurotexis* appears to be due to convergence. This is a condition which has been evolved many times in the acalyptrates. It does, however, confirm the distinction of *Nothoasteia* from subgenus *Neurochaeta*, in which the second basal cell is consistently separated from the discal cell and confluent with the first basal cell.

Nothoasteia resembles species of subgenus *Neurochaeta* in several characters which are associated with flattening of the thorax. The partly almost planate sternopleuron with a series of upper, anterior bristles is such a character, as is the short, flat scutellum and bulging subscutellum. But in the groundplan of the genus *Neurochaeta* the thoracic flattening is less developed, as are these associated apomorphic characters. This indicates a complex convergence between *Nothoasteia* and the more apomorphic forms of *Neurochaeta*. Loss of certain bristles, e.g. the postvertical and supra-alar, also constitutes convergence between *Nothoasteia* and subgenus *Neurochaeta*, but, on the whole, reduction in chaetotaxy has progressed further in the former.

I conclude from the above morphological evidence that *Nothoasteia* separated from the main neurochaetid stem certainly before the divergence of subgenera *Neurotexis* and *Neurochaeta*, probably before the separation of subgenus *Neurocytta*, and possibly earlier than the stage reached by the fossil *Anthoclusia*. The very marked autapomorphies of *Nothoasteia* (including the flattened head, setulose eyes, presence of mesopleural setulae, modifications of the furcasternum, sternopleura, and metasternum, loss of tarsal claws, loss of costal break, almost total fusion of subcosta and vein 1, loss of alular fringe, divided sternite 7 of the female abdomen) suggest that the separation from other forms may be particularly early in the history of the Neurochaetidae. Those apomorphies have, however, had a transforming effect on the insect as a whole and make its accurate placement in the phylogenetic system impossible at present.

Geographic origins

The Neurochaetidae are at present distributed in wetter parts of the Old World tropics and subtropics, and there is no evidence that they have occurred in the New World.

Anthoclusia, which fulfils morphological requirements for a stem group to genus *Neurochaeta* (and possibly to *Nothoasteia*), occurred in northern Europe in the late Eocene or the commencement of the Oligocene. The genus *Neurochaeta* was apparently derived from a species which had acquired further apomorphies (McAlpine, 1978). *Anthoclusia* lived at a time when Africa was still separated from Europe by the Tethys Sea, and judging from the meagre but probably significant evidence from mammalian fossils

(Coryndon and Savage, 1973), European land fauna did not invade Africa until well into the Oligocene. If early neurochaetids were strictly inhabitants of moist forest, like their descendants, they were probably no more vagile than land mammals. It is probable therefore that *Anthoclusia* was restricted to Eurasia at the Eocene-Oligocene boundary, and the two separate lineages (subgenera *Neurocytta* and *Neurotexis*), which are now in the Afrotropical Region, reached there some time later in the Tertiary. Until better collections of Afrotropical neurochaetids are made no significant comparison can be made between the faunas of Madagascar and the African mainland.

The restriction of the Australasian species to the vicinity of rainforest in tropical and subtropical areas, together with their similarity to oriental species, indicates a late arrival in Australasia, perhaps during the Pliocene when sea barriers to the north were at a minimum.

The distribution of *Nothoasteia* is little known, but its occurrence in southwestern Australia suggests that the genus is part of an older Australian fauna, without indicating more precisely the time of its occupation.

KEY TO RECENT GENERA OF NEUROCHAETIDAE

Eye setulose; costa unbroken; alula without fringe; functional tarsal claws absent	*Nothoasteia*
Eye without obvious setulae; costa with break at end of subcosta; alula with marginal fringe; tarsal claws developed	*Neurochaeta*

GENUS *NEUROCHAETA* MCALPINE

Neurochaeta McAlpine, 1978: 278-281. Type-species *N. inversa* McAlpine.

Five species have been added to this genus since its description (Woodley, 1982, and the present work), but these are all rather closely related to the type-species and are referable to the same subgenus. Despite doubt as to the phylogenetic position of the species of *Nothoasteia* in relation to the *Neurochaeta* species, there is no persuasive evidence that *Neurochaeta* s.l. is polyphyletic. The afrotropical species, *N. prisca* and *N. stuckenbergi*, are at present known to me from a miniscule sample of three specimens, which may not be sufficient to indicate the diversity of the fauna and consistency of group characters. Nevertheless, as shown above, these species are phylogenetically isolated from other known neurochaetids and are now considered to require their own subgenera.

Key to subgenera of *Neurochaeta*

1	Second basal cell completely enclosed; upper posterior sternopleural bristles 2; scutellar bristles of major pair approximated near apex of scutellum; subscutellum not prominent	*Neurocytta*
—	Second basal cell incomplete; upper posterior sternopleural bristle solitary; scutellar bristles of major pair widely separated; subscutellum very convex and prominent	2
2	Second basal cell confluent with discal cell; costa terminating at vein 3; radial sector without bristles; postvertical, presutural, and supra-alar bristles present; suborbital bristle absent; posterior margin of scutellum bare between major bristles	*Neurotexis*
—	Second basal cell confluent with first basal cell; costa terminating at vein 4; radial sector towards base with 2 to 4 strong erect bristles; presutural, supra-alar, and usually, postvertical bristles absent; suborbital bristle usually present; posterior margin of scutellum with one or more pairs of shorter bristles between major pair	*Neurochaeta*

Subgenus *Neurocytta* n. subg.

Type species: *Neurochaeta prisca* McAlpine.

Fronto-orbital bristles 4, one of which is inserted mesad of and a little behind foremost of the aligned series; short postvertical bristle present; cheek with one postgenal bristle situated behind lowermost point of eye (not homologous with suborbital bristle of subgenus *Neurochaeta*). Presutural bristle absent; one dorsocentral bristle present; supra-alar bristle present; scutellar bristles of major pair approximated near apex of scutellum; scutellum otherwise with short lateral hairs only; postnotum receding below scutellum, not prominent; sternopleuron with 2 upper posterior bristles and no anterior bristles. Wing with strong, spaced anterior bristles on costa between terminations of veins 1 and 2; costa extending to termination of vein 4, with simple break at termination of subcosta; macrotrichia on radial sector represented by small hairs on stem of veins 2 and 3 dorsally; second basal cell separated from both first basal and discal cells; anal cell completely enclosed; vein 6 well developed beyond anal cell; alula relatively broad. Postabdomen of male with large, asymmetrically placed sternites 6 and 7, dorsal sternite 8, and well developed epandrium; cercus in both sexes inconspicuous, not plate-like.

The distinctive characters of the only included species of *Neurocytta*, viz. *Neurochaeta prisca*, and their phylogenetic significance have been discussed by McAlpine (1978) and Woodley (1982). This species is still only known from the type material from Zimbabwe.

The subgeneric name is derived from the Greek *νευϱον*, nerve or wing-vein, and *ϰυτταϱος*, cell in reference to the well developed cells in the basal part of the wing. It is feminine on account of the ending.

Subgenus *Neurotexis* n. subg.

Type species: *Neurochaeta stuckenbergi* McAlpine.

Fronto-orbital bristles 4, the inclinate one inserted mesad of and at same level as anterior reclinate one; postvertical bristle present; one postgenal bristle as in *Neurocytta*; suborbital bristle absent. Presutural bristle present; dorsocentral bristles 2; supra-alar bristle present; scutellar bristles in 2 pairs: widely separated major pair, and shorter lateral pair; subscutellum deep and convexly prominent; sternopleuron with one upper posterior and no anterior bristles. Costa terminating immediately beyond end of vein 3, with fairly strong spaced anteroventral bristles between terminations of veins 1 and 2, without short erect dorsal setulae immediately before end of subcosta; costal section before subcostal break produced distally in front of break as a long, finger-like process; radial sector without macrotrichia; second basal cell separate from first basal cell, confluent with discal cell; anal cell small, imperfectly enclosed; vein 6 little developed beyond anal cell; alula rather narrow. Postabdomen of male unknown; cercus of female narrow, subcylindrical.

The characters and relationships of the only included species are discussed by McAlpine (1978) and Woodley (1982). It is only known from the unique holotype from Madagascar.

The subgeneric name is derived from the Greek *νευϱον*, a nerve or wing-vein, and *τεξις*, a wasting or dissolution, in reference to the distal fading of the costa and vein 4. It is feminine.

Subgenus *Neurochaeta* s. str.

Fronto-orbital bristles 3, the inclinate one situated in front and mesad of foremost reclinate one; postvertical bristle absent (except in *N. magnifica*); a variable series of postgenal bristles present along posterior margin of eye; suborbital bristle present below lowest point of eye (Figs 18, 26; reduced in *N. magnifica*, Fig. 25); one dorsocentral or 2 approximated bristles present; supra-alar (as distinct from postalar) bristle absent; scutellar bristles of major pair sublateral on posterior margin, with shorter intermediate bristles or hairs on posterior margin and pair of anterolateral bristles; postnotum largely occupied by the convexly prominent subscutellum; sternopleuron with one upper posterior bristle and with either a variable series of bristles or a number of bristly hairs anteriorly. Wing with variable, usually rather weak, spaced anterodorsal and anteroventral bristles on costa between terminations of veins 1 and 3; costa extending to end of vein 4, often with obliquely incised break at termination of subcosta, but not with long process as in *Neurotexis*; macrotrichia on radial sector represented by normally 2 or 3 strong bristles; second basal cell confluent with first basal cell, separated from discal cell; anal cell and vein 6 variably developed, the former always narrow; alula moderately developed or rather narrow. Asymmetrical sternites of protandrium reduced or absent; epandrium reduced to a transverse, usually medially narrowed plate; surstylus detached from margin of protandrium.

This subgenus includes 6 known species from the Oriental and Australian Regions.

Key to species of subgenus *Neurochaeta*

1 Head depressed, longer than high; inner vertical bristle absent; anterior crossvein well before middle of length of discal cell; prosternum very broad; hypopleuron setulose; hind femur much longer than thorax; host apparently *Pandanus* (*magnifica* group) . . . . *magnifica*

— Head not longer than high; inner vertical bristle well developed; anterior crossvein near or beyond middle of length of discal cell; prosternum attenuated; hypopleuron bare; hind femur not longer than thorax 2

2 Vein 5 not continued beyond discal cell; anterior sternopleural bristles in a well developed series, pale yellowish; prosternum very narrowly linear; metasternum extensively setulose; mid coxae separated from one another by at least the width of each coxa; mid femur with loose comb of ventral bristles on basal half; scutellum with one pair of shorter bristles between major pair of bristles on posterior margin; suborbital bristle curved downwards; ♂ postabdomen with sternite 8 present but very short (condition unconfirmed for *N. sabroskyi*) (*parviceps* group) 3

— Vein 5 continued beyond discal cell; spaced dorsal setulae of costa fine and sharp; anterior sternoplural bristles black or undifferentiated; prosternum lanceolate; metasternum bare or with minute inconspicuous setulae; mid coxae separated from one another by much less than width of each; mid femur without distinct ventral comb; scutellum with 2 or more pairs of bristles or setulae between major pair of bristles on posterior margin; suborbital bristle curved outwards; ♂ postabdomen with sternite 8 nearly as long as tergite 6 or absent 5

3 Femora pale yellowish, except for dark apical part of hind one; fore coxa not distinctly keeled; abdomen with large pale yellowish zone covering tergites 1, 2, and anterior margin of 3; length of dorsocentral bristle not more than half length of scutellum; discal cell at distal end slightly narrower than marginal cell at same level; host apparently *Alocasia* . . . . *macalpinei*

— Femora largely black; fore coxa with strong anterodorsal keel distally; abdomen with pale yellowish basal zone less extensive or absent; length of dorsocentral bristle more than half length of scutellum; discal cell at distal end slightly broader than marginal cell at same level 4

4 Abdominal tergite 1 pale yellowish, contrasting with darker rest of abdomen; capitellum of haltere creamy white; thorax much wider than head; wing less than twice as long as thorax, and less than 3 times as long as wide; host apparently *Zingiber* . . . . *parviceps*

— Abdominal tergite 1 brownish, not strongly contrasting with rest of abdomen; capitellum of haltere tawny; thorax about as wide as head; wing more than twice as long as thorax, and more than 3 times as long as wide; host unknown . . . . *sabroskyi*

5 Sclerotized section of vein 6 present beyond anal cell; anal cell completely enclosed; mid femur without anteroventral bristle; anterior sternopleural bristles not differentiated from hairs; a short second dorsocentral bristle close in front of major one; cercus not broad and plate-like; sternite 8 of ♂ large, nearly as long as tergite 6; host apparently *Musa* (*capilo* group) . . . . *capilo*

— Vein 6 scarcely discernible beyond anal cell; anal cell vestigial; mid femur with short anteroventral bristle; some anterior sternopleural bristles fairly long; only one dorsocentral bristle present; cercus in both sexes broad, plate-like, exserted; sternite 8 of ♂ absent; host *Alocasia* (*inversa* group) . . . . *inversa*

Capilo Group n. gr.

Suborbital bristle curved outwards; prelabrum moderately developed; humeral callus compact; propleural callus rather small, convex, not sharply defined below; palpus rather long; prementum narrow; thorax not much depressed; scutellum with minor bristles and hairs between major pair of bristles not in a transverse row; upper margin of subscutellum incurved, not inflexed; anterior sternopleural bristles not differentiated from coarse hairs; prosternum rather broadly lanceolate; metasternum bare; mid coxae broad, approximated; mid femur with neither anteroventral bristle nor ventral comb; tarsal claws long and attenuated, each as long as last tarsal segment; vein 5 extending beyond discal cell; anal cell complete; vein 6 developed beyond anal cell; sternite 8 of male large; cercus in both sexes neither plate-like nor posteriorly exserted.

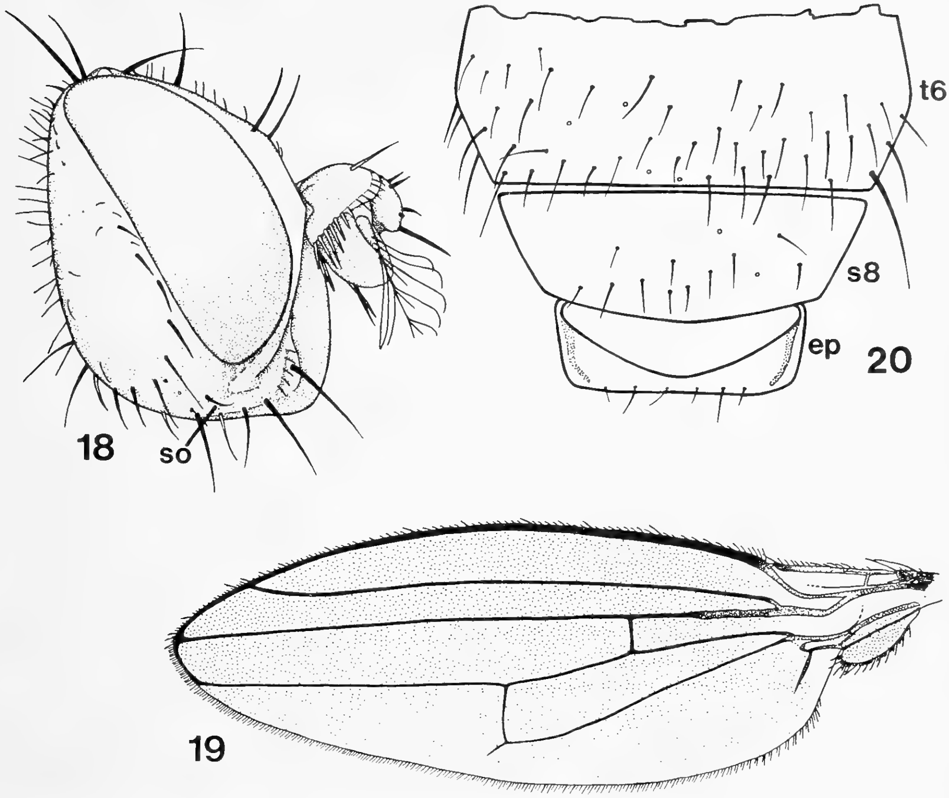
This group is at present monotypic. It occurs in the Oriental Region.

Neurochaeta capilo n.sp.

(Figs 8, 10, 13, 18-21)

♂ ♀. Resembling *N. inversa* and agreeing with description given for that species (McAlpine, 1978) except as indicated below.

Coloration: Head greyish brown; parafacial and anterior margin of postfrons orange-fulvous; postocular zone pale grey; antenna and many of its bristles and setulae creamy white; setulae of antennal segment 1 and those on inner surface of segment 2 black; one major dorsal and ventral bristle on segment 2 black or brown; arista beyond base brown. Thorax greyish brown, paler in parts. Hind coxa pale yellowish; other coxae greyish brown; femora brown, fore one pale yellowish basally and apically, mid and hind ones pale yellowish basally; fore tibia yellowish apically; fore tarsus yellowish; other tarsi predominantly brown or hind one paler basally. Wing with whitish zone



Figs 18-20. Neurochaeta capilo. 18. Head. 19. Wing (ventral). 20. Dorsal sclerites of male postabdomen (not compressed). ep = epandrium. so = suborbital bristle. s8 = sternite 8. t6 = tergite 6.

extending to extreme base, but distally extending only slightly beyond forks of veins 2 and 3, and 4 and 5; alula tinged with brown. Haltere pale creamy, more yellowish on scabellum.

Head. Height of cheek about 0.15 of height of eye; postfrons a little concave medially but without narrow median channel; eye less oblique than in other species of subgenus; incurved fronto-orbital bristle inserted only slightly anteriorly to anterior reclinate fronto-orbital.

Thorax less depressed than in other species of subgenus; 2 dorsocentral bristles present, anterior one short and close to posterior one, sometimes little differentiated; scutellum with bristles of major pair sublateral, also a much shorter lateral and convergent posterior pair present in addition to several fine dorsal setulae towards apex; upper anterior sternopleural bristles not differentiated from coarse black hairs of this region. Fore coxa not markedly compressed, without anterodorsal keel; mid femur without anteroventral bristle; hind femur with one long dorsal and one anteroventral (rather than anterior) bristle beyond middle. Costa with black bristle terminating basal section and series of anterodorsal setulae preceding it much stouter than in other species of subgenus, and with pale subterminal dorsal setula absent (or represented by a weak more basally placed setula); costal index 4.8-4.9 (♂), 5.1-6.3 (♀); vein 4 index 2.6-3.0 (♂), 1.9-2.4 (♀); anal cell narrow, enclosed distally by curved crossvein; vein 6 well sclerotized for some distance beyond anal cell.

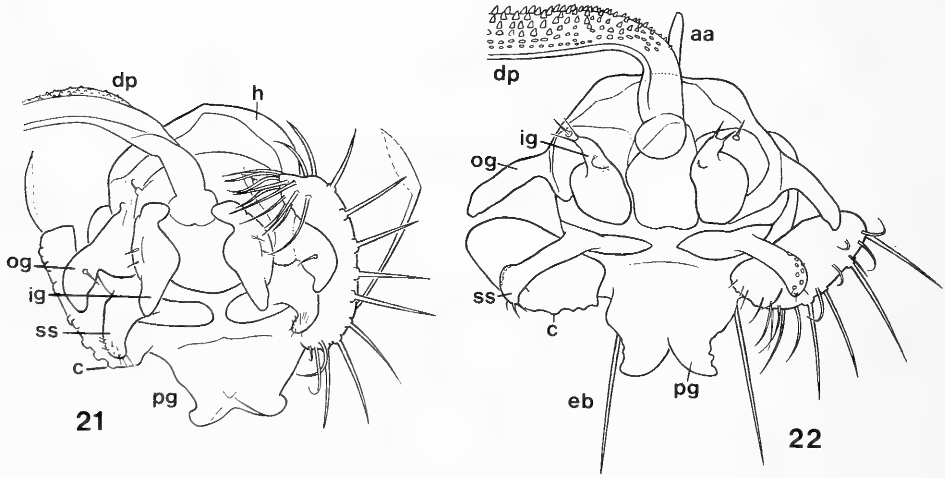
Abdomen more slender and slightly less depressed than in *N. parviceps*, tergites 2-6 each with submarginal lateral groove and a bristle on lateral margin which is no more than half as long as tergite. ♂ postabdomen: sternite 6 much reduced, on left side, mirrored by a much smaller sclerite on right side; sternite 7 less reduced than sternite 6, fused to left lateral margin of sternite 8; sternite 8 a little shorter than tergite 6, with several fine setulae; epandrium much narrowed medially, produced at anterolateral angles, with 6 fine setulae on posterior margin; surstylus becoming slender beyond basal plate, with minute apical hairs; outer gonite with posteriorly directed apex and one setula on inner surface; inner gonite much expanded distally into an anterior and a posterior process, with 2 setulae on outer surface; basiphallus short, sclerotized; distiphallus exceedingly long and slender, membranous, with one longitudinal pigmented strip, membranous part towards base with numerous weak, minute denticles, apical part not thickened; cercus elongate, passing forwards from its base and decurved apically, with a series of long bristles along outer surface and fascicle of finer bristles at apex. ♀ postabdomen: cercus very short and inconspicuous, apparently ovoid, with few, minute setulae.

Dimensions: total length, ♂ 2.7-3.2mm, ♀ 2.6-3.1 mm; length of thorax, ♂ 1.1-1.3 mm, ♀ 1.0-1.1mm; length of wing, ♂ 2.5-2.8mm, ♀ 2.3-2.7mm; length of distiphallus c. 3.6mm.

Distribution: West Malaysia — Selangor.

Holotype ♀: Old Bentong Pass, E of Gombak, 15.iv.1985 (Australian Museum), K. C. Khoo and D. K. McAlpine.

Paratypes: same locality, 15-16.iv.1985, 14.viii.1986 (1 ♀ British Museum (Natural History), 2 ♂, 2 ♀, Australian Museum), same collectors.



Figs 21, 22. Genital segment, ventral aspect (only base of distiphallus shown, setation omitted from right cercus). 21. *Neurochaeta capilo.* 22. *N. parviceps.* aa = aedeagal apodeme. c = cercus. dp = distiphallus. eb = epandrial bristle. h = hypandrium. ig = inner gonite. og = outer gonite. pg = proctiger. ss = surstylus.

N. capilo differs from other species of subgenus *Neurochaeta* in its less depressed thorax, undifferentiated anterior sternopleural bristles, distinct curved anal crossvein closing anal cell and presence of sclerotized vein 6 beyond this cell, narrow forwardly bent cercus in ♂ and small inconspicuous cercus in ♀.

Inversa Group

Inner vertical bristle present; suborbital bristle curved outwards; prelabrum moderately developed; palpus well developed but rather short; prementum rather narrow; thorax moderately depressed; humeral callus rather elongate, but without slender anterior prolongation; propleuron with well developed convex callus defined below by a shallow depression; scutellum with transverse series of 4 to 8 posterior bristles between major pair; upper margin of subscutellum inflexed throughout; anterior sternopleural bristles in a definite series, black, tapered; hypopleuron bare; prosternum more or less lanceolate, but slightly variable; metasternum with at most few minute setulae which are difficult to distinguish from pubescence; mid coxae separated by distinctly less than width of each coxa; mid femur with short anteroventral bristle, without ventral comb; tarsal claws moderately long and strong, slightly shorter than terminal segment on each tarsus; vein 5 extending beyond discal cell; anal cell reduced, not distinctly closed distally; vein 6 undeveloped beyond anal cell; cerci of both sexes exserted, broad and plate-like.

Woodley (1982) introduced the *inversa* group to include *Neurochaeta inversa* McAlpine, *N. sabroskyi* Woodley, and *N. macalpinei* Woodley. With the addition of three more species, this concept is raised to a subgenus, and only the Australian *N. inversa* remains in the redefined *inversa* group.

Neurochaeta inversa (Fig. 1) is the best known species in the family and has been the subject of biological and ecological studies (McAlpine, 1978: Shaw, Cantrell, and Houston, 1982; Shaw and Cantrell, 1983a, 1983b).

Magnifica Group n.gr.

Inner vertical bristle absent; suborbital bristle vestigial or absent; prelabrum moderately developed; palpus well developed but rather short; prementum as in *inversa* group, but more strongly bristled; thorax greatly depressed; humeral callus rather compact, not anteriorly prolonged; propleural callus large, strongly convex, as deep as humeral callus, separated from ventral section of propleuron by a deep groove; anterior notopleural bristle closer to posterior notopleural than to humeral callus, situated higher above notopleural suture than is posterior notopleural; scutellum with transverse series of 7 to 14 short posterior bristles between major pair; upper margin of subscutellum strongly inflexed throughout; anterior sternopleural bristles in an irregular series, black, tapered; hypopleuron with few fine setulae; prosternum very broad; metasternum strongly setulose; mid coxae separated by much more than width of each coxa; mid femur without well defined ventral comb; tarsal claws moderately long and strong, those of mid tarsus shorter; costal armature simplified; vein 5 extending well beyond discal cell; anal cell reduced; vein 6 not visible beyond anal cell; cerci of both sexes exserted, broad and plate-like.

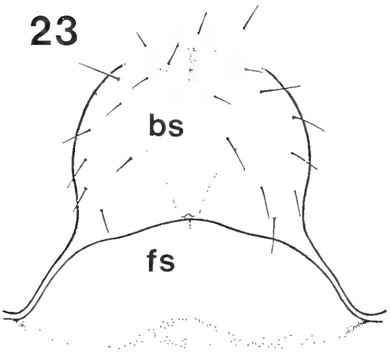
The only known species of the group is much the largest of neurochaetids. It is the only neurochaetid yet known from New Guinea.

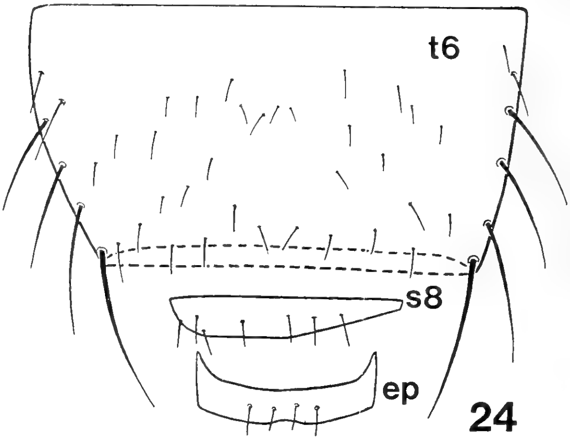
Neurochaeta magnifica n.sp.

(Figs 15, 23-25)

♂ ♀. With the group characters given above, otherwise agreeing with description given for *N. inversa* (see McAlpine, 1978) except as indicated below.

23





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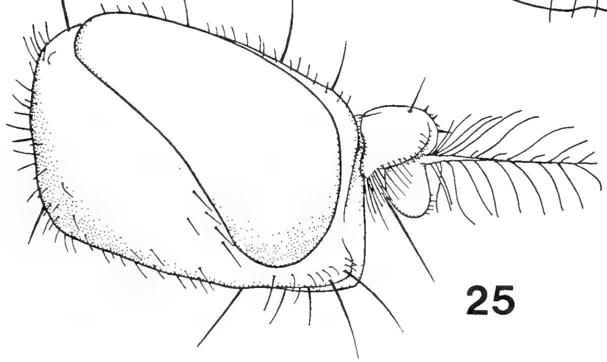

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Figs 23-25. Neurochaeta magnifica. 23. Prosternum. 24. Dorsal sclerites of male postabdomen (not compressed). 25. Head. bs = basisternum. ep = epandrium. fs = furcasternum. s8 = sternite 8. t6 = tergite 6.

Coloration: head brown-black with grey pruinescence; face mid-brown; eye, after relaxation of freshly dried specimen, rich coppery purple; antenna brown; prelabrum and palpus dark brown; hairs and bristles on head and its appendages black, except for pale hairs on labella and antennal segment 3. Thorax coloured as in *N. inversa*. Mid coxa blackish; other coxae largely brown; femora brown-black, often darker distally; tibiae and tarsi black. Wing smoky brown, becoming paler posteriorly and sub-basally, but without paler zones except in immature specimens; alula dark. Haltere dark brown. Abdomen almost entirely dark brown (tergites 1-9 in ♀); cercus creamy with silvery pruinescence.

Head more depressed than in other species of genus; eye longer than high, with posterior margin sinuate-oblique; postfrons more narrowed posteriorly than in other species, with narrow, deep median groove in front of anterior ocellus; cheek c. 0.06-0.11 of height of eye; postvertical bristles apparently represented by a pair of convergent, approximated setulae far behind vertex; ocellar bristles very small; anterior and posterior fronto-orbital bristles markedly shorter than intermediate one, the anterior ones less medially inclined than in other species (sometimes almost parallel). Antennal sockets more widely separated than in *N. inversa* and *N. parviceps*, only slightly more so than in *N. capilo.*

Thorax flatter than in other species (including *N. parviceps*), anteriorly narrowed; scutellum more broadly flattened than in other species, shorter than in *parviceps* group. Fore coxa not keeled; fore femur stouter than in other species, greatly swollen basally, slightly concave on anterodorsal surface; other femora more elongate than in other species, the hind one much the larger; mid femur with several short anterior to anteroventral bristles; hind femur distally with one anterior and one or 2 posterodorsal bristles; mid and, particularly, hind tibiae, and mid tarsus unusually slender. Costal section on second costal cell with 2 rows of distally lengthening black setulae but without additional dorsal setulae just before subcostal break; costal section on marginal cell with 3 rows of closely placed black setulae for most of length, without widely spaced anterodorsal and anteroventral bristles (weak in *N. inversa*); veins 3 and 4 distally convergent; costal section between veins 3 and 4 three times as long as anterior crossvein, which is well basad of middle of discal cell; costal index 5.2-5.9; vein 4 index 1.3-1.4.

Abdomen. Sternites broader than in other species, in ♀ sternites 4-6 as broad as tergites, in ♂ 4 and 5 slightly narrower. ♂ postabdomen: segment 6 with large, slightly asymmetrical tergite, with well developed symmetrically placed and formed ventral sclerite on each side, the left member of this pair apparently representing sternite 6, each of these sclerites with one long bristle and one or 2 setulae; sternite 8 reduced, asymmetrical, setulose; epandrium somewhat reduced, with 4 fine setulae only, which are not mounted on tubercles; surstylus strongly but gradually expanded basally, with basal plate less developed than in other species of subgenus, particularly on anterior side, with several setulae, mainly on posterior side well before apex, which is blunt but not thickened; outer gonite short, broad, tapered, strongly setulose; inner gonite broad, not lobed, subtruncate, incurved, with 3 setigerous tubercles on outer surface; distiphallus only moderately slender, with well developed triangular teeth, much less numerous than in *N. parviceps*, on about basal third; cercus broadly ovate-rhomboid, with bristles much shorter than in *N. inversa* and *N. parviceps*.

Dimensions: total length, ♂ 5.2mm, ♀ 4.5-5.8mm; length of thorax, ♂ 1.9mm, ♀ 1.5-2.1mm; length of wing, ♂ 4.9mm, ♀ 3.9-5.0mm; length of distiphallus c. 1.5mm.

Distribution: Papua New Guinea — Western Highlands Province.

Holotype ♀: Mur Mur Pass, 2760m, on *Pandanus* leaf, 15.iii.1986 (Australian Museum), J. W. Ismay.

Paratypes: same data as holotype, 1 ♂, 2 ♀, Australian Museum, 1 ♀ British Museum (Natural History), 1 ♀ National Museum of Natural History, Washington, 3 ♀ Department of Primary Industry, Konedobu.

Notes: N. magnifica differs from all other known neurochaetids in its large size and broad prosternum. It differs from all other species of the genus *Neurochaeta* in the absence of the inner vertical bristles, the posterodorsal displacement of the anterior notopleural bristle, and in having the hind femur much longer than the thorax.

Parviceps Group n.gr.

Inner vertical bristle present; suborbital bristle curved downwards; prelabrum much reduced; palpus very short; prementum broad; thorax much depressed; humeral callus markedly elongate, with slender anterior prolongation; propleuron without callus; scutellum without hairs or additional bristles between major pair of bristles; upper margin of subscutellum not inflexed; anterior sternopleural bristles in curved series, yellowish, scarcely tapered; prosternum narrow-linear; metasternum with well developed setulae; mid coxae separated by at least width of each coxa; mid femur usually with short anteroventral bristle before middle and loose ventral comb basally; tarsal claws short, on hind tarsus not more than ⅔ as long as terminal tarsal segment;

vein 5 not extending beyond discal cell, which has its posterodistal angle rounded off; anal cell reduced, not distinctly closed distally; vein 6 undeveloped beyond anal cell; cerci of both sexes exserted, broad and plate-like.

This group includes 3 known species, viz. *N. sabroskyi*, *N. parviceps*, and *N. macalpinei*. All are oriental.

Neurochaeta sabroskyi Woodley

Neurochaeta sabroskyi Woodley, 1982: 211-212, fig. 1.

This species has the characters of the *parviceps* group, but the thorax is more slender and the wing more elongate than in other species of the group. It is distinguishable from *N. parviceps* and *N. macalpinei* by the characters given in the key.

Distribution: Philippines — Mindanao.

Material examined: holotype ♀ (Museum of Comparative Zoology, Harvard).

Neurochaeta macalpinei Woodley

Neurochaeta macalpinei Woodley, 1982: 212-214, fig. 2.

This species has the characters of the *parviceps* group, but differs from the other two species in its paler coloration and shortening of certain bristles, including the scutellars, though the humeral and both notopleural bristles are long.

Male postabdominal characters resemble those of *N. parviceps*. The pair of long bristles on sternite 8 is not quite as long; the surstylus is not capitate at the apex; the outer gonite is more slender and falcate; the inner gonite has a very short acute outer lobe and a more elongate curved inner lobe bearing two preapical setulae; the aedeagus has cuticular teeth almost as well developed as those of *N. parviceps*; there is one particularly strong bristle on each cercus, the other bristles being mostly much smaller.

Distribution: East Malaysia — Sabah.

Material examined: holotype ♂ and 19 paratypes (Australian Museum).

Neurochaeta parviceps n.sp.

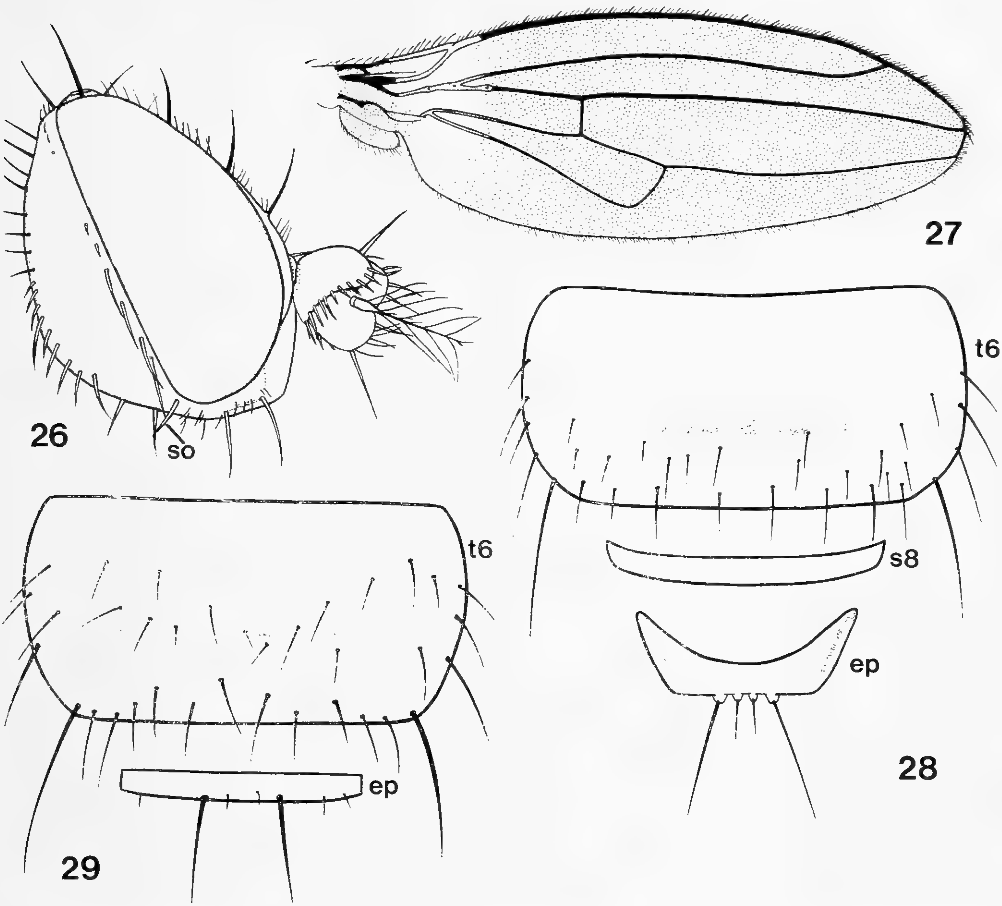
(Figs 5, 11, 16, 22, 26-28)

♂ ♀. Resembling *N. inversa* and agreeing with description given for that species (McAlpine, 1978), except as indicated below and in the characters given for the *parviceps* group.

Coloration: Anterior margin of postfrons, face, and anterior part of cheek creamy white; cheek bristles predominantly yellowish (♂) or blackish (♀). Antenna, including bristles, entirely pale yellowish except for brown distal part of arista; palpus brown, paler distally. Thorax blackish with very thin greyish pruinescence; postscutellum silvery, as in *N. inversa*. Legs darker than in *N. inversa*; mid and hind femora very narrowly yellowish at bases; fore tibia yellowish, with brownish zone before middle; mid and hind tibiae black, with narrowly yellowish apices. Wing coloured as in *N. inversa*, but with pale sub-basal zone smaller and less distinct; haltere brown basally, with whitish capitellum.

Head more anteroposteriorly compressed than in *N. inversa*, with postfrons longer in proportion to face and cheek narrower; postfrons concave, with linear median channel; inner vertical bristle notably shorter than outer vertical; anterior fronto-orbital bristle somewhat closer to ptilinal suture than to next fronto-orbital; suborbital bristle curved downwards. Bristles and setulae on antennal segment 2 much stronger than in *N. inversa*. Prelabrum vestigial; palpus very short; prementum broader than in other species.

Thorax remarkably broad and flat, narrowed anteriorly; humeral callus remarkably prolonged anteriorly; scutellum a little longer than in *N. inversa*, with only one pair of



Figs 26-29. Neurochaeta parviceps. 26. Head. 27. Wing (ventral). 28. Dorsal sclerites of male postabdomen. 29. *Neurochaeta inversa*, dorsal sclerites of male postabdomen. ep = epandrium. so = suborbital bristle. s8 = sternite 8. t6 = tergite 6.

marginal bristles and no hairs between the major bristle pair; pleura much excavated between anterior notopleural bristle and fore coxa; anterior sternopleural bristles 5 to 8 in a curved series, directed ventrally; sclerotized prosternal plate even narrower than in *N. inversa*; metasternum with numerous distinct setulae. Fore coxa more compressed than in *N. inversa*, with distinct anterodorsal keel on distal part; mid coxae separated by slightly more than width of one coxa (separated by about 0.7 of that width in *N. inversa*); hind femur somewhat curved on basal part (straight in *N. inversa*), with oblique series of short anterodorsal to dorsal bristles well before middle, a short anteroventral bristle just beyond middle, and a long dorsal bristle just beyond this. Costa, between humeral crossvein and subcostal break, with setulae of anterodorsal and anteroventral series all black, short, moderately stout and sharp, both series only slightly increasing in size distally, in addition one thick, blunt, yellowish dorsal setula at apex of section before subcostal break and a similar dorsal setula (occasionally 2 setulae) a little basad of this; vein 4 distally attenuated, strongly converging with vein 3; costal index 4.2-4.8; vein 4 index 2.8-3.2.

Abdomen: ♂ postabdomen: sternite 8 much reduced, glabrous, transversely elongate; epandrium somewhat reduced, with pair of long bristles and pair of fine setulae arising from tubercles on posterior margin; surstylus rather slender beyond basal plate, almost straight, slightly thickened at apex, with minute setulae near apex only; outer gonite not as slender as in *N. inversa*, but more so than in *N. capilo*, glabrous; inner gonite bilobed apically, but much more narrowly so than in *N. capilo*, with 2 setulae at apex of anterior lobe; distiphallus elongate, but stouter than in *N. inversa* and *N. capilo* and much shorter than in the latter, with rather numerous strong, short teeth on surface, instead of the weak denticles of those species; cercus somewhat as in *N. inversa*. Cercus of ♀ somewhat as in *N. inversa*, with one posteriorly directed bristle longer and more prominent than other bristles.

Dimensions: total length, ♂ 2.9-3.2mm, ♀ 3.0-3.2mm; length of thorax, ♂ 1.3-1.4mm, ♀ 1.3-1.4mm; length of wing, ♂ 2.4-2.6mm, ♀ 2.5-2.6mm; length of distiphallus c. 0.9mm.

Distribution: West Malaysia — Selangor.

Holotype ♂: Old Bentong Pass, E of Gombak, 16.iv.1985 (Australian Museum), K. C. Khoo and D. K. McAlpine.

Paratypes: same locality, 14-16.iv.1985, 22 ♂, 2 ♀, Australian Museum, 1 ♂, 1 ♀, British Museum (Natural History), 1 ♂ Canadian National Collection, Ottawa, 1 ♂ National Museum of Natural History, Washington, 1 ♂, Természettudományi Múzeum, Budapest.

Notes: N. parviceps differs from the other two species of the *parviceps* group in having the head significantly narrower than the thorax. It further differs from *N. macalpinei* in the darker femora and longer dorsocentral and scutellar bristles, and differs from *N. sabroskyi* in the entirely pale bristles on antennal segment 2 and the broadly flattened thorax.

GENUS ***NOTHOASTEIA*** MALLOCH

Nothoasteia Malloch, 1936: 259. Type species *N. platycephala* Malloch.

The following are the essential characters of the genus so far as they are understood at present. The detailed description given for *N. clausa* no doubt includes some characters which will be found to be generic rather than specific when a better range of material becomes available.

Head much depressed, with reduced bristling; outer vertical bristle developed; no anterior incurved fronto-orbital bristle distinguishable; eye horizontally elongate, its surface setulose except towards posterior extremity; ocelli rather widely spaced, lateral ones at posterior limit of postfrons; antennal segment 2 less enlarged and cucullate than in *Neurochaeta*, more as in *Anthoclusia*; thoracic bristling reduced; humeral callus compact, rounded, very prominent, with few setulae and a weak posteriorly directed bristle; metasternum elongate, bare, separated from hypopleuron on each side by membrane of hind coxal cavity (broader than long and continuously sclerotized with hypopleuron in front of coxal cavity in *Neurochaeta*); mid leg remarkably small; hind coxae short, inserted on each side of metasternum (inserted behind metasternum in *Neurochaeta*); tarsi without functional claws; costa unbroken; second basal cell confluent with discal cell, separate from first basal cell; anal cell wide open distally; vein 6 strongly sclerotized, though not reaching margin; haltere with elongate capitellum.

Only two specimens of *Nothoasteia* are known, but these are from remote localities in southern Queensland and southwestern Australia respectively. This, together with the fact that the two specimens represent two species, suggests the possibility that the genus has a wide distribution over Australia and includes numerous species. Perhaps, when some clues as to the ecology of the insects become available, significant data on distribution and species diversity may be obtained. The characters given in the above description have been confirmed for both species of the genus.

Key to species of *Nothoasteia*

1	Discal cell widely open; hind tibia pale yellowish, faintly browned apically	*platycephala*
—	Discal cell closed distally, narrower than submarginal cell; hind tibia brownish on much of length with isolated dark brown apical zone . . .	*clausa*

Nothoasteia clausa n.sp.

(Figs 6, 12, 30)

♀. *Coloration.* Head with its appendages and macrotrichia pale yellowish; postfrons largely brownish, with pale pruinescence and pale yellowish anterior margin; ocellar region darker. Thorax brownish, darkest dorsally, with yellowish macrotrichia; mesoscutum and scutellum densely pruinescent; humeral callus and parts of pleura yellowish, the latter somewhat shining. Legs yellowish; hind femur with ill-defined brownish distal zone; terminal segment only of each tarsus brownish. Wing with yellowish veins and unpigmented membrane. Haltere pale yellow. Abdomen yellowish brown, paler ventrally.

Head apparently slightly wider than long; outer vertical bristle short but distinct, somewhat proclinate; inner vertical bristle perhaps represented by a short proclinate setula slightly in front of a straight line drawn from lateral ocellus to postvertical bristle; ocellar bristles represented by pair of fine proclinate, subparallel setulae; frontal orbit with a series of several short, mostly proclinate setulae and, a little in front of middle, one moderately fine bristle sloped somewhat forwards and outwards; median part of postfrons with proclinate setulae, mostly on anterior half; frontal lunule concealed; face shallow and apparently rather narrow (collapsed); cheek region rather broad, largely facing ventrally in anterior part, much expanding posteriorly, with rather numerous long proclinate setulae anteriorly, among which some possibly represent peristomal bristles; eye with numerous procurved setulae, which are little developed on posterior part. Antenna with segment 1 short and simple; segment 2 setulose, particularly on inner side, with deep dorsolateral slit distally, with distal surface facing ventrally; segment 3 probably oval and apically rounded (collapsed), without long hairs; arista minutely pubescent throughout, more densely so towards base, with basal segments (4 and 5) apparently very short (4, if present, not visible without preparation). Prelabrum rather weak; palpus moderately short; proboscis rather short with moderately developed prementum; labella separated from one another by a deep anterior slit (labella fused in *Neurochaeta*), each anteriorly truncate, with about 9 dentate pseudotracheae.

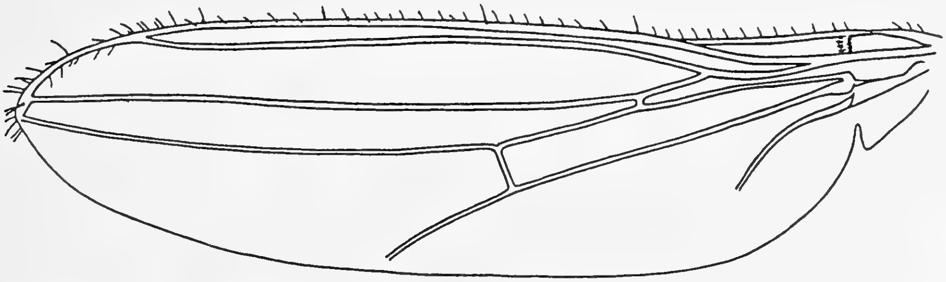


Fig. 30. Nothoasteia clausa, wing (dorsal).

Thorax slender, rather convex above, ventrally rather planate, so that much of sternopleural region faces ventrally; 2 weak notopleural bristles present, anterior one slightly further from notopleural suture than is posterior one; a much smaller bristle or strong setula in approximately presutural or posthumeral position; mesocutum apparently without further differentiated bristles, with sparsely scattered short setulae, those on anterior part directed posteriorly (as usual), most of those on posterior half directed anteriorly; scutellar suture deeply and narrowly incised; scutellum very short, flat-topped, with free margin narrowly convex and with evenly rounded outline, with bristles reduced to 3 pairs of small, medially inclined, submarginal setulae, those of apical pair not widely separated; postnotum shallower than in most *Neurochaeta* spp., almost evenly convexly prominent; propleuron without evident bristles or setulae; mesopleuron with several relatively long bristles on posterior half, not concentrated near posterior margin; upper posterior sternopleural bristle represented by a minute setula; upper anterior sternopleural bristles fairly long, about 6 in a horizontal series, with apices apparently directed posteriorly; sternopleuron otherwise with scattered setulae; prosternal plate (basisternum) absent, but anteriorly angular prothoracic furcasternum distinct as in *Neurochaeta* (the latter perhaps mistaken for prosternal plate by Malloch, 1936). Legs having greater disparity of size than in most species of *Neurochaeta*; fore coxa with several anterior setulae, but no anterior basal bristle; femora, tibiae, and tarsi rather irregularly haired; fore femur with a few dorsal bristles; tarsi depressed distally, with normal pulvilli; claws not visible under high magnification; one or 2 short ciliate hairs terminating fore and mid tarsi perhaps representing claw vestiges. Wing surface entirely densely microtrichose; costa unbroken, thickened apically between veins 3 and 4, on section bordering costal cell with a series of regular slightly spaced setulae, beyond vein 1 with numerous setulae or hairs, which are very diverse and irregular in size and position, on last 2 sections (beyond vein 2) with an irregular series of ventral setulae, and on dorsal surface near centre of terminal section with one rather strong setula; humeral crossvein ill defined; subcosta almost totally fused with stem vein and vein 1, visible ventrally as a ridge along anterior margin of this vein-complex, which is expanded where it joins costa; marginal cell narrow, in part no wider than thickness of vein 2; veins 3 and 4 apically convergent; anterior crossvein very short so that veins 3 and 4 are approximated at this point; discal cell rather narrow, almost parallel-sided on much of its length; terminal section of vein 5 almost as long as penultimate section of vein 4; posterior marginal fringe rather long, not reaching vicinity of alula; alula moderately developed, subacute; costal index c. 4.9; vein 4 index 3.4. Haltere with remarkably elongate capitellum.

Abdomen slender apparently subcylindrical (not depressed as in *Neurochaeta*); tergites up to tergite 6 large but lightly sclerotized, with reduced bristling; pleural membrane thrown into telescopic folds at junctions of segments 2 to 6, as is intersegmental membrane; sternite 1 vestigial; sternites 2 to 6 rather broad, the more anterior ones weakly sclerotized; sternite 7 completely divided longitudinally on median line, more strongly setulose than preceding sternites; cercus not distinctly visible, probably very small.

Dimensions: total length 2.2mm; length of thorax 0.74mm; length of wing 2.0mm.

Distribution: Western Australia — southwest district south of Perth.

Holotype ♀ (unique): Yaragil 4P Catchment, via Dwellingup, 20-27.xi.1980 (Australian Museum), A. C. Postle. Malaise trap.

Notes: M. R. Gray, who knows the vicinity of the type locality, informs me that it is likely to be in dry sclerophyll forest.

This new species is conspicuously different from *N. platycephala* in venation, as the discal cell is closed and veins 4 and 5 are subparallel beyond the anterior crossvein, only commencing to diverge distad from the discal crossvein. The shape of the marginal cell also differs, being narrowest in its mid region in *N. clausa*.

The above description has some shortcomings due to the condition of the unique type, which has also prevented presentation of a satisfactory set of illustrations. Because the cuticle is lightly sclerotized, the head has collapsed; also the thorax is damaged by the pin. I have carefully examined the displaced sections of the thoracic cuticle on the right side and believe my account of the thoracic chaetotaxy to be accurate.

Nothoasteia platycephala Malloch

Nothoasteia platycephala Malloch, 1936: 259-260, figs. 1, 2, 2a.

The following are supplementary notes on the unsexed holotype. Its condition does not enable production of a formal description.

Coloration: Postfrons apparently with pale yellow orbital margins more differentiated than in *N. clausa*. Mesoscutum (at least anteriorly) blackish, much darker than in *N. clausa*. Legs pale yellowish; hind femur with very diffuse pale brownish distal zone; hind tibia pale creamy, with indistinct pale brownish suffusion on distal fifth only; each tarsus with slightly browned distal segment.

Wing: Marginal cell narrow, but no narrower near middle than it is distally; vein 2 shorter than in *N. clausa*; veins 4 and 5 diverging throughout, quite strongly so on region just beyond anterior crossvein; discal crossvein absent, no trace or indication of its position remaining.

Material examined: Holotype, unsexed, 'Brisbane, Qld', no other original data; 'damaged in transit. F. H. Taylor'. The head, with damaged antennae, is glued by its ventral surface to the card and there is some glue on the postfrons. Much of the thorax is destroyed but the anterodorsal part and the metasternal region are visible. Detached legs and both wings are glued to the card. Only the base of the abdomen remains.

GENERA AND SPECIES OF NEUROCHAETIDAE

Genus *Anthoclusia* Hennig, 1965
    A. gephyrea Hennig, 1965. Palaearctic (Eocene-Oligocene)
    A. remotinervis Hennig, 1969. Palaearctic (Eocene-Oligocene)
Genus *Neurochaeta* McAlpine, 1978
Subgenus *Neurocytta* n. sg.
    N. prisca McAlpine, 1978. Afrotropical: Zimbabwe
Subgenus *Neurotexis* n. sg.
    N. stuckenbergi McAlpine, 1978. Afrotropical: Madagascar
Subgenus *Neurochaeta* s. str.
    N. capilo n. sp. Oriental: W. Malaysia
    N. inversa McAlpine, 1978. Australasian: Australia
    N. magnifica n. sp. Australasian: N.E. New Guinea
    N. sabroskyi Woodley, 1982. Oriental: Philippines
    N. parviceps n. sp. Oriental: W. Malaysia
    N. macalpinei Woodley, 1982. Oriental: E. Malaysia
Genus *Nothoasteia* Malloch, 1936
    N. clausa n. sp. Australasian: Western Australia
    N. platycephala Malloch, 1936. Australasian: Queensland

ACKNOWLEDGEMENTS

I am particularly indebted to K. C. Khoo for assistance with fieldwork both in Australia and Malaysia. J. W. Ismay collected and forwarded the material of *Neurochaeta magnifica*. M. Robinson, B. G. Duckworth, D. S. Kent, and A. Bowman prepared most of the illustrations. D. J. Bickel critically read the manuscript. N. E. Woodley arranged for loan of the type of *Neurochaeta sabroskyi*.

References

COLLESS, D. H., and MCALPINE, D. K., 1970. — Chapter 34. Diptera. In *The insects of Australia*: 656-740. Melbourne: Melbourne University Press.

CORYNDON, D. H., and SAVAGE, R. J., 1973. — The origin and affinities of African mammal faunas. *In* HUGHES, N. F., (ed.): *Organisms and continents through time*: 121-135. London: Palaeontological Association.

CRAMPTON, G. C., 1942. — The external morphology of the Diptera. *Bull. Conn. geol. nat. Hist. Surv.* 64: 10-165.

GRIFFITHS, G. C. D., 1972. — *The phylogenetic classification of Diptera Schizophora with special reference to the structure of the male postabdomen*. The Hague: W. Junk. 340 pp.

HARDY, G. H., 1950. — On the articulating scutellum in Diptera. *Ent. mon. Mag.* 86: 230.

HENNIG, W., 1958. — Die Familien der Diptera Schizophora und ihre phylogenetischen Verwandtschaftsbeziehungen. *Beitr. Ent.* 8: 505-688.

——, 1965. — Die Acalyptratae des Baltischen Bernsteins und ihre Bedeutung für die Erforschung der phylogenetischen Entwicklung dieser Diptera-Gruppe. *Stuttgart. Beitr. Naturk.* 145: 215pp.

——, 1969. — Neue Übersicht über die aus dem Baltischen Bernstein bekannten Acalyptratae. *Stuttgart. Beitr. Naturk.* 209: 42pp.

MCALPINE, D. K. 1973. — The Australian Platystomatidae (Diptera, Schizophora) with a revision of five genera. *Mem. Aust. Mus.* 15: 256pp.

——, 1978. — Description and biology of a new genus of flies representing a new family (Diptera, Schizophora, Neurochaetidae). *Ann. Natal Mus.* 23: 273-295.

MALLOCH, J. R., 1936. — Notes on Australian Diptera. XXXVI. *Proc. Linn. Soc. N.S.W.* 51: 259-261.

SHAW, D. E., and CANTRELL, B. K., 1983a. — A study of pollination of *Alocasia macrorrhiza* (L.) G. Don (Araceae) in southeast Queensland. *Proc. Linn. Soc. N.S.W.* 106: 323-335.

——, and ——, 1983b. — Further notes on seed set in *Alocasia macrorrhiza* (Araceae) and occurrence of *Neurochaeta inversa* (Diptera: Neurochaetidae) in Queensland. *Qd Nat.* 24: 71-75.

——, and ——, and HOUSTON, K. J., 1982. — *Neurochaeta inversa* McAlpine (Diptera: Neurochaetidae) and seed set in *Alocasia macrorrhiza* (L.) G. Don (Araceae) in southeast Queensland. *Proc. Linn. Soc. N.S.W.* 106: 67-82.

WOODLEY, N. E., 1982. — Two new species of *Neurochaeta* McAlpine (Diptera: Neurochaetidae), with notes on cladistic relationships within the genus. *Mem. ent. Soc. Wash.* 10: 211-218.

Studies in Upside-down Flies (Diptera: Neurochaetidae) Part II. Biology, Adaptations, and specific mating Mechanisms

DAVID K. MCALPINE

McALPINE, D. K. Studies in upside-down flies (Diptera: Neurochaetidae). (Part II. Biology, adaptation, and specific mating mechanisms. *Proc. Linn. Soc. N.S.W.* 110 (1), (1987) 1988: 59-82.

Field observations and apparent host plants (families Araceae, Musaceae, Pandanaceae, and Zingiberaceae) are recorded for some species. Pollen-feeding is recorded for adult *Neurochaeta inversa*. Aspects of adult morphology and behaviour are considered in relation to adaptation, in particular to running (including running backwards), infrequent flight, living in crevices, adult longevity, specialization and reduction of options, ecological advantages of 'upside-down' behaviour, and diversity of male postabdominal morphology (including evolution of the protandrium). Male postabdominal diversity in general is here placed in the category of *specific mating mechanisms*. This common but little understood concept is compared critically with the premating isolating mechanism concept and the specific mate recognition system concept. The legitimacy of seeking Darwinian explanations for morphological specializations is discussed.

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manuscript received 21 May 1986, accepted for publication 22 July 1987.

INTRODUCTION

Part I of this study (McAlpine, 1988) dealt with the systematics and phylogeny of the Neurochaetidae, including the genera *Neurochaeta*, *Nothoasteia* and the extinct *Anthoclusia*. Some information on biology, behaviour, and ecology of the Australian *Neurochaeta inversa* McAlpine has been given by McAlpine (1978), Shaw, Cantrell, and Houston (1982), and Shaw and Cantrell (1983).

Neurochaeta inversa and the East Malaysian *N. macalpinei* Woodley (1982) are both associated with the araceous plant *Alocasia macrorrhiza* (L.) G. Don. Apparent host plants belonging in other families are here recorded. These are all large monocotyledons, perhaps all providing some kind of phytotelma in which the larvae may be expected to live. It is probable that adaptation to the host microhabitat has influenced some of the morphological peculiarities and diversity of adult Neurochaetidae, but variation in other characters, particularly those of the male postabdomen, is paralleled in other dipterous families and may be a by-product of the speciation process.

FIELD OBSERVATIONS (WEST MALAYSIA)

Neurochaetids were observed by K. C. Khoo and the author in rain forest along the Old Bentong Pass road between Gombak village and Genting Highlands turnoff on 14-16 April 1985.

Adults of *Neurochaeta parviceps* were found in small numbers on peduncles of the club-shaped young inflorescences of wild ginger, *Zingiber spectabile* Griff. Several other species of ginger (Zingiberaceae) were flowering in the area, but no neurochaetids could be found on them. These flies moved in the characteristic upside-down mode of the genus (see McAlpine, 1978), very rapidly when pressed, and their elusive movements made them difficult to capture with an aspirator, though aspiration proved the most effective method of capture. They sometimes sheltered in the small cavities of the stem bracts, but never in the floral bracts which were always brim-full of rain water. When disturbed they eventually ran, or more rarely flew, to other parts of the plant. If persistently pursued they sometimes left the plant altogether. A mating pair of *N. parviceps* was seen by Khoo on a *Zingiber* plant.

In this habitat some specimens of *Neurochaeta capilo* were also collected. These were consistently on the leaf blades and petioles of wild banana (*Musa* sp., Musaceae). A few specimens of *N. parviceps* also found on the banana were possibly recently disturbed from an adjacent ginger plant. Only certain plants of *Musa* in the areas appeared attractive to *N. capilo*, and there was evidence of repeated return of probably the same individual to such plants. One of these attractive plants supported numerous specimens of *Formicosepsis*, otherwise scarce in the area, and there was frequent non-aggressive contact between these and *Neurochaeta*.

OBSERVATIONS ON *NEUROCHAETA MAGNIFICA* IN PAPUA NEW GUINEA

J. W. Ismay reports as follows (*in litt.*): 'I was collecting at Mur Mur Pass in the Tomba Gap at approximately 143°59′E, 5°50′S [2760m]. . . . The area had been partly cleared but some young *Pandanus* were left. The *Neurochaeta* were seen on the inside of upright leaves of *Pandanus*, walking up and down with the head always downwards. They ranged to the tops of the leaves. The silver markings on the back of the head and behind the scutellum were conspicuous against their dark coloration. Some were caught by sweeping a net against the leaves, but most, when approached, ran down the leaf base and were pooted. They were at least as fast as *N. inversa*, which I have taken in Queensland.'

HOST PLANTS

All specimens of *Neurochaeta parviceps* were found on or near *Zingiber spectabile*. At the time only young inflorescences were present, none having reached anthesis. These young inflorescences terminate in a cluster of bracts, each of which remains full of rainwater, because of the almost daily rainfall and low evaporation rate. Several kinds of dipterous larvae were found in this liquid from three sampled inflorescences, but none of these could be identified as *Neurochaeta* from comparison with the known third-instar larva of *N. inversa*, though some very small, probably first-instar cyclorrhaphous larvae were found. I do not regard this as strong evidence that the larvae of *N. parviceps* do not live in the water trapped in the bracts of *Zingiber*; on the contrary I think that at a later stage of development this is most likely to be the larval habitat.

The sample of *N. parviceps* obtained by Khoo and me has the unexpected sex ratio of 31 males to 3 females. The biological significance of this is not apparent.

The strong attraction of adults of *Neurochaeta capilo* to plants of wild banana (*Musa* sp.) is established by observations recorded above. If this species is as closely associated with a host species in all stages as is *N. inversa*, then *Musa* would seem to be the larval host, but those plants on which the flies were found had closely appressed petiole bases, leaving no axillary cavities, and no inflorescences. At the time the adults were collected, only a very small percentage of *Musa* plants had inflorescences and these appeared to have no actual or potential water-holding parts. *Musa* plants are, however, often reported to provide phytotelmata.

The identity of the *Pandanus* host of *Neurochaeta magnifica* is uncertain. Ismay was informed by a villager that the plants were 'karuka', a name used in Papua New Guinea to designate *Pandanus* spp. useful for production of thatching and matting, and also for their edible fruits. In highland areas of Papua New Guinea, *Pandanus jiulianettii* and *P.*

brosimos are the principal 'karuka' species and their fruits are an important local food source (Stone, 1982). *P. brosimos* occurs in the Tomba vicinity close to the type locality of *Neurochaeta magnifica* (Stone, 1982: figs 6, 7) and may be the host of this fly, but this is only one of about 66 species of *Pandanus* known from New Guinea.

Stone also states: 'The pandan leaf axil is of considerable interest. It is usually stocked by the infall of detritus from above, usually retains water to the extent of a cupful or more, or a thick solution of decaying debris, and may incorporate dying fragments of the endo-axillary rootlet system.' Among the invertebrates living in this habitat he mentions larvae of cyclorrhaphous flies. Thus this appears to be a likely habitat for the larvae of *Neurochaeta magnifica*. However, Ismay (*in litt.*) points out: 'Since the [karuka] palms are 10-30m high and very spiny, few entomologists collect from them. Also, they cannot be tampered with — damage to karuka is a common cause of tribal conflict in the Highlands'.

FEEDING IN *NEUROCHAETA INVERSA*

At Mount Tenison Woods, D'Aguilar Range, near Brisbane, Queensland, on 4.ii.1983, K. C. Khoo and I observed inflorescences of *Alocasia macrorrhiza* being visited by three species of insects, all taking pollen from the spadix. These were *Neurochaeta inversa*, *Trigona* sp. (apparently *T. carbonaria* Smith, det. E. Exley, a native social bee) and *Apis mellifera* L. The last species was in the smallest numbers, but tended to disturb or disperse the others when present. Clearly, higher concentrations of *A. mellifera* would have inhibited seriously the activities of the other two species.

We observed numbers of *N. inversa* adults repeatedly licking the surface of the male section of the spadix and apparently ingesting pollen. On a number of occasions the flies were seen to approach the hind leg of a *Trigona* and actively lick at the pollen load. The *Trigona*, in each case, attempted to withdraw its leg or move away, but the fly often followed to some extent.

While *Alocasia* pollen provides a high protein food source for *N. inversa*, this food is available only during the summer flowering period of the plant. My previous conjecture, that the flies feed on various substances collected on the large leaves of *Alocasia*, is supported by further observations (Border Ranges National Park, near Kyogle, N.S.W., 3.iv.1987). Periods of running activity on leaf surfaces were interrupted at intervals when the flies began licking at spots of unidentified substances on the leaf surface. When drops of diluted orange-marmalade were smeared in their paths, the flies stopped to feed on it. Thus the leaf-surface activity is to be interpreted as foraging.

LOCOMOTION AND LEG STRUCTURE

I have described for *N. inversa* (McAlpine, 1978) the habit of running rapidly backwards and forwards with constant head-downwards orientation while on a vertical surface. This habit is now also recorded for a further four species of the subgenus *Neurochaeta*, viz. *N. parviceps* and *N. capilo* (observations by K. C. Khoo and author), *N. macalpinei* (observations reported to author by J. Frazier and D. Clyne, noted Woodley, 1982), and *N. magnifica* (Ismay's observations). Almost certainly the fifth species of the subgenus, *N. sabroskyi*, has the same habit.

The speed and the erratic nature of running are remarkable in subgenus *Neurochaeta* for such small insects. I have observed a specimen of *N. inversa* to run at an average speed of about 3.7cm/sec for a period of 30sec, during which time the direction of movement was reversed about 50 times. Under similar conditions an active specimen of *Stenomicra* sp. of similar size moved at about 1.2cm/sec with only about 6 fairly abrupt reversals of direction in 30sec.

The specialized running mechanism of *Neurochaeta* appears to have certain advantages in: (1) avoiding predators, (2) finding scarce food substances by covering a large area of plant surface in a short time, (3) seeking out small apertures (e.g. for escape from plant cavities), (4) the searching out of conspecific individuals in aggregation and perhaps in sexual activity.

Differentiation of the leg proportions is characteristic of the family. These are particularly expressed in the relative size of the femora and the general description is as follows: fore femur short and stout; mid femur short and slender; hind femur long and moderately stout; tibia of each leg shorter than femur. The precise proportions of the femora vary between the species as shown in Table 1. The fossil *Anthoclusia gephyrea* has the least differentiation in femoral length, according to the scale drawings of Hennig (1965: figs 251, 252), and this appears to be the most plesiomorphic condition known in the family. *Neurochaeta magnifica* and the species of *Nothoasteia*, on the other hand, have the greatest differentiation. The reduction of the mid legs in *Nothoasteia* is reminiscent of that of wingless males of the hymenopterous family Agaonidae.

It seems logical to relate the unusual leg proportions of neurochaetid flies to the mode of locomotion which is characteristic of all observed species, even though present knowledge does not explain the mechanistic aspects of this relationship.

TABLE 1

Relative lengths of femora in neurochaetids

Ratios fore femur: mid femur: hind femur

A. gephyrea	♂. 1: 1.1: 1.4	♀. -
Ne. capilo	♂. 1: 1.2: 1.8	♀. 1: 1.2: c.1.9
Ne. inversa	♂. 1: 1.1: 1.9	♀. 1: 1.1: 1.9
Ne. magnifica	♂. 1: 1.2: 2.7	♀. 1: 1.2: 2.6
Ne. sabroskyi	♂. -	♀. 1: 1.0: 1.9
Ne. parviceps	♂. 1: 1.1: 1.9	♀. 1: 1.0: 1.9
Ne. macalpinei	♂. 1: 1.0: 1.8	♀. 1: 1.0: 1.8
No. clausa	♂. -	♀. 1: 0.7: 2.1
No. platycephala	?. 1: 0.8: 1.9	

Flies of the genus *Nothoasteia* are remarkable and perhaps unique among the Schizophora in the absence of anything in the nature of a tarsal claw. Because tarsal claws are so generally present in Diptera, it is certain that they fulfil a function in their biology which cannot normally be dispensed with. Presumably the primary function is clinging to surfaces, which are either rough or sufficiently soft for an impression to be made by the sharp claw apex. One might, then, infer that *Nothoasteia* normally lives on surfaces which offer no such opportunity for gripping with claws, such as a hard, smooth surface or a loose powdery one. The paired pulvilli are well developed on all tarsi of *Nothoasteia*, as in other neurochaetids. These are pads of sticky hairs which enable most flies to cling to and walk on smooth surfaces, even if the surface is vertical or facing downwards (e.g. a window pane or ceiling). They do not function on wet surfaces (so far as known). If non-sticky, these pads could aid walking on a powdery surface.

While absence of functional claws may seem to set *Nothoasteia* apart from the rest of the Neurochaetidae, there is variation in claw size between species of the subgenus *Neurochaeta*. Also there may be variation in claw size in the one individual, those of the smaller mid legs often being slightly smaller than those of the large hind legs. *Neurochaeta capilo* and *N. parviceps* are flies of similar size, but the hind tarsal claws of the former are at least twice as long as those of the latter species. The other species of the *parviceps* group have claws of similar proportions to those of *N. parviceps*, but *N. inversa* has claws intermediate in size between those of the *capilo* and *parviceps* groups.

The strong, moderate-sized claws of *Neurochaeta inversa* are similar to those of periscelidids and many other small acalyptrate flies, and probably approximate to the plesiomorphic condition for the *Neurochaetidae.* The elongate, needle-like condition in *N. capilo* and the shortened condition of the claws in the *parviceps* group appear to be apomorphies which have developed in opposite directions. Claw reduction in *Nothoasteia* is clearly independent of and convergent with that in the *parviceps* group. The adaptational significance of this reduction may become clearer when studies are made of living *Nothoasteia*.

RUNNING BACKWARDS

The orientation of the hairs and bristles on the dorsal surface of flies with apices directed posteriorly is apparently an adaptation to walking (and probably to flying) forwards with minimal resistance. Though several (perhaps all) species of *Neurochaeta* walk backwards as much as they walk forwards (and probably for much longer periods than they fly forwards), the orientation of most hairs and bristles remains as in strictly forward-walking flies, though a few of the dorsal bristles are sometimes nearly erect. These longer bristles would tend to shield the posterior mesoscutal hairs from contacting any obstacle dorsal to the insect. By contrast the hairs on the median region of the posterior half of the mesoscutum in *Nothoasteia clausa* are directed forwards, those on the anterior part being largely directed backwards; most bristles are quite short and there are no long posteriorly directed ones. In the absence of behavioural records of this rare fly, this condition suggests that the backward locomotion may be at least as important as forward locomotion in *Nothoasteia.* The legs of *Nothoasteia* are similar to those of some apomorphic types found in *Neurochaeta*, e.g. in *N. parviceps*, particularly in the long hind femora and reduction in size of the mid legs; also the body-form is strongly depressed, and reduction of the prosternal plate has extended to complete loss. These features suggest behavioural similarity in the two groups. Because *Nothoasteia* has not acquired apomorphic wing-venational characters present in the groundplan of subgenus *Neurochaeta*, it is evident that the extreme developments of the legs and body-form have been acquired independently in the two groups. As the developments are mostly present in a less elaborated state in such plesiomorphic neurochaetids as *Anthoclusia* and subgenus *Neurocytta*, it is not surprising that similar states of elaboration should have been achieved in different lineages.

Concentration of organs of vision on the anterior end in insects is an obvious adaptation to forward locomotion, perhaps particularly to forward flight as non-flying cursorial insects (e.g. worker ants) generally have reduced eyes. Because, in subgenus *Neurochaeta*, running backwards is a more frequent occupation than forward flight, one might expect some modification of vision in connection with this behaviour.

In all the species of the genus *Neurochaeta* the eyes are obliquely elongate. Thus, though total area of the eye is not great, there is a larger number of ommatidia facing dorsally than in other cursorial flies (such as phorids, and certain sphaerocerids). In living examples of *N. inversa* and *N. parviceps*, there is a characteristic concave-backed profile resulting from the head being held away from the substrate through dorsal flexion at the neck. This unusual position contrasts with that of dried specimens, and careful examination shows that several ommatidia would then provide some vision in a posterior to posterodorsal direction. The convex posterior extremity of the eye in *N. magnifica* could also increase posterior vision.

Previously (McAlpine, 1983) I recorded observations indicating that the aulacigastrid flies *Nemo centriseta* McAlpine and *Nemo kentae* McAlpine walk consistently forward, while *N. corticeus* McAlpine and *N. phaeotylos* McAlpine often walk backwards and forwards with abrupt reversals of direction at short intervals. I have recently examined the eyes of these four species, and find that the posterodorsal margin of the eye in the two latter species is extended slightly further on to the posterior surface of the head and has the marginal ommatidia directed slightly more in a posterior direction than in the former pair of species. Firm conclusions as to this apparent connection between behaviour and structure require more observations on *Nemo* spp. than those yet made. Except for *N. centriseta*, the observations have been few, and the morphological difference between the two species pairs is small. However, if such a connection is proved for *Nemo*, this would strengthen the expectation of comparable adaptations in *Neurochaeta*, where backward motion is a more significant element of behaviour.

In neurochaetids the parts projecting furthest posteriorly, and therefore those which usually make first contact with an obstacle in running backwards, are the wing tips and the tip of the abdomen. In the subgenus *Neurochaeta* and in *Nothoasteia* the wing tips have special hairs or setulae which could be tactile. In the former they form a small, compact group at the apex of vein 3; in *Nothoasteia* these setulae are not in such a compact group, and the short section of the costa bearing them, between veins 3 and 4, is remarkably thickened. This thickening could be a strengthening device in a part subject to battering when the insect runs backwards.

In most species of the subgenus *Neurochaeta* the cerci of both sexes are broadened, exserted, and fringed with long setulae. The possibility of these structures acting as tactile organs and buffers for running backwards could explain why the cerci, which usually have evolved along different lines in each sex, have here evolved the same apomorphic condition in both sexes. *N. capilo* is the only species of the subgenus *Neurochaeta* with cerci short (in female) or not posteriorly prominent (in male), although it is capable of running backwards at speed. This species is apparently a sister group to the rest of the subgenus, and has probably never acquired these apparently adaptive attributes, despite an equally long history of running backwards. This condition of the cerci is perhaps explained by the insect having larger wings, a further plesiomorphic character.

Nothoasteia also lacks modifications of the cerci or other apical abdominal parts. In *Neurochaeta capilo* and *Nothoasteia* the greater size of the wings relative to the abdomen renders it less probable that the abdomen would make first contact with an obstacle. Perhaps also *N. capilo* lives in a more open habitat than *N. inversa*, *N. parviceps*, and *N. macalpinei*, and is thus less likely to run into objects.

Examples of adaptation for running backwards as well as forwards in other animals seem to occur mainly in types living in tunnels or burrows, where it can be advantageous to reverse direction of locomotion without turning the body. Moles of the genus *Talpa* (Mammalia: Insectivora) are reported to run as fast backwards as forwards (Boonsong and McNeely, 1977). The fur of moles is soft and velvety, and can lie in any direction, enabling the animals to go backwards and forwards in a burrow without the grain of the fur giving resistance. These facts prompt comparison with *Nothoasteia* and raise the questions: Does *Nothoasteia* live in tunnels or burrows? Can its dorsal thoracic setulae have their direction reversed, like moles' fur, or is their position, as described above, permanent? In *Talpa micrura* Hodgson the tail is much reduced, but acts as a sensory organ when it is running backwards. This compares with the posterior sensory organs of *Nothoasteia* and subgenus *Neurochaeta*.

FAST FORWARD LOCOMOTION

In view of the presence of apparent adaptations for rapid backward movement, comparable adaptations for forward movement in neurochaetids should also be considered, as forward running appears to be just as frequent and rapid as backward running. As mentioned above, forward vision is well developed. Forwardly directed vibrissae are present in *Neurochaeta*, but the anterior parts most liable to the effects of collision are the antennae. Antennal segment 3 is presumably furnished with the usual complex and delicate array of sense organs found in higher Diptera, including chemoreceptors. The rather long hairs on the anterior surface of this segment would afford some protection to these organs in *Neurochaeta*, and segment 3 is particularly well protected from physical contact with surrounding objects by the large, cucullate segment 2, which, in subgenus *Neurochaeta*, bears strong anterior bristles. The arista projects further forwards than other parts of the antenna and could serve to sense an imminent collision rather than to shield physically other parts from contact.

In species of subgenus *Neurochaeta*, which, so far as known, tend to flex the head upwards, the anteriorly inclined median ocellus would be unable to receive stimulation from a light source directly in front of the insect, were it not for the fact that the postfrons has a median channel leading to the space between the antennae. In some species, e.g. *N. magnifica* and *N. parviceps* it is scarcely wider than the ocellus, very well defined, and commences immediately in front of the ocellus.

INFREQUENT FLIGHT

Observations on species of the subgenus *Neurochaeta* seem to indicate that running is a more frequently used escape mechanism than flying and that flight is an infrequently used form of locomotion. Nevertheless all species for which we have field observations can fly (i.e. all species except *N. sabroskyi*), and flight is probably necessary for dispersal to new host plants. *N. macalpinei* shows reduction of the wing area, which is probably an indication of the lesser importance of flight in its biology. Comparison of the wings in *N. macalpinei* and *N. parviceps* suggest that the latter also has undergone slight reduction of the wing and that the loss of the free distal part of vein 5 is an element of this reduction (also occurring in a third species, *N. sabroskyi*, with slightly longer but narrower wing). *N. parviceps* often seemed most reluctant to fly in the field, probably more so than *N. capilo* which lacks these indications of wing-reduction (though field observations on the latter species were restricted to few individuals).

N. macalpinei not only shows the greatest wing reduction of any known *Neurochaeta* species, but also the most marked shortening of many of the bristles, notably the fronto-orbitals, dorsocentrals, and scutellars, though the notopleurals are quite long. There seems a possibility that the bristle-shortening is an adaptation to infrequent flight, though the importance of bristles in flight is not well understood. On the other hand *Nothosteia* species show a much greater bristle reduction without apparent reduction of wing area. This is not just a reduction in length, but an overall reduction in size and number of the bristles, and,in parts, also a reduction of the hairs. The case of *Neurochaeta macalpinei* is reminiscent of the genera *Baeopterus* (Coelopidae) and *Calycopteryx* (Micropezidae), both flightless examples with shortened bristles in families of normally actively flying forms.

LIVING IN CREVICES

I have already concluded (McAlpine, 1978) that in *Neurochaeta inversa* the dorsoventrally compressed body is an adaptation to moving through narrow spaces, such as are provided by the host plant, *Alocasia*. This ability has been confirmed on two occasions when several adults of *N. inversa* escaped from a collecting jar by way of the thread of the screw-top, which had an imperfect inner seal. By comparison, *N. capilo* is much less depressed. Perhaps, if *Musa* is the only host of this species, then there is less necessity and opportunity for creeping into narrow spaces. One individual, apparently of *N. capilo*, when pursued, was seen to shelter in the channel on the adaxial side of the banana petiole, but this was a relatively open and capacious hollow.

Neurochaeta parviceps has a more strongly depressed body than other *Neurochaeta* species which I have observed in the field, though in *N. macalpinei* it is almost as depressed and in *N. magnifica* more so. *N. parviceps* has been seen to shelter in the narrow and shallow spaces in the axils of the bracts on the peduncles of young inflorescences of *Zingiber spectabile*. A reduced depth of the thoracic region by comparison with *N. inversa* is partly achieved through reduction in size of the mid coxae and their migration from near the median line to a more lateral position on the thorax. This results in a greater ventral exposure of the metasternum (which in *N. inversa* tends to be concealed by the mid trochanters). In the *parviceps* and *magnifica* groups the ventrally directed anterior sternopleural bristles and the setulae on the metasternum are particularly well developed, in response, I believe, to the need for feeling the substrate in an insect in which the thorax is held unusually close to it.

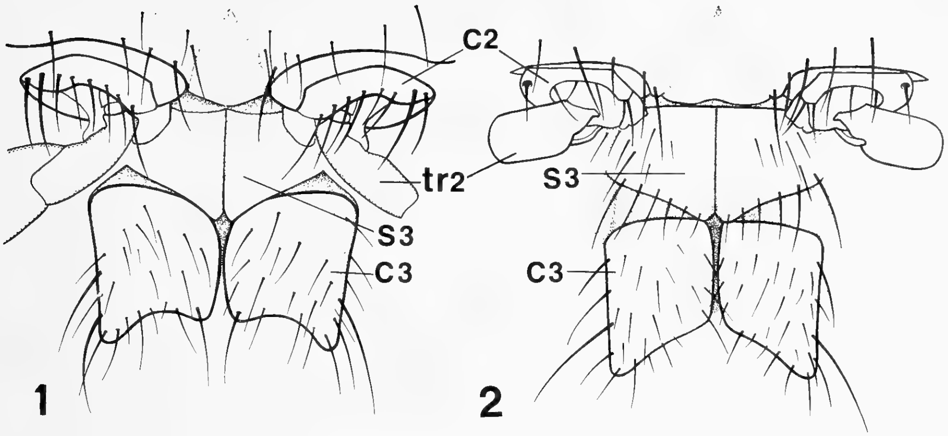
The thoracic pleura of *N. parviceps* and to some extent those of related species (including *N. inversa*) have, laterally to the fore coxa, a marked ventrally facing hollow, which appears to enable relatively free movement of the laterally splayed fore legs, without their occupying space between the thorax and the substrate.

The size and apparent resting position of the fore coxa, as evidenced from dried material, varies among species of Neurochaetidae, and these attributes relate to the variations in structure of the prothoracic furcasternum. In *Neurochaeta capilo* the furcasternum is not prominent and is covered by the more or less distally contiguous, bulky fore coxae. The coxae appear to work largely below the sternal region of the thorax, occupying a significant part of the depth of the insect. In *N. parviceps* the broad, flat furcasternum rather widely separates the more laterally placed fore coxae. The coxae are less bulky than in *N. capilo*, compressed, keeled, and apparently adapted for movement within the pleural hollow without occupying much space below the thorax. In *N. inversa* the condition is intermediate between that of *N. capilo* and *N. parviceps*. The furcasternum is rather narrowly convex and the coxae, though decidedly separated at rest, are generally less so than in *N. parviceps*. The condition in *N. macalpinei* and *N. sabroskyi* is similar to that of *N. parviceps*, but in the former the rather small coxae are neither compressed nor keeled.

In *Neurochaeta magnifica* the structure and co-adaptation of these prothoracic parts are quite different from the above types. The problem of the working of the forelegs under a remarkably shallow thorax has been solved by a migration of the coxa almost to the lateral extremity of the thorax, the section of the pleura above it being almost vertical and exceedingly shallow to accommodate the coxa. With the fore coxae extremely distant from each other and the prothoracic pleura quite limited to the lateral surfaces of the thorax, there remains a ventral prothoracic surface much broader and more open than in other species. The furcasternum is thus even broader than in *N. parviceps*, and the very broad prosternal plate is unlike that of any other neurochaetid.

In *Nothoasteia clausa* the condition of the fore coxae most resembles that of *Neurochaeta macalpinei*, but there is no pleural hollow.

In contrast to the mid coxa, mobility of the fore coxa is essential to the operation of the leg in locomotion; hence the quite different nature of its specialization.



Figs 1, 2. Metasternum and surrounding parts of *Neurochaeta* spp. 1. *N. inversa.* 2. *N. parviceps.* c2 = mid coxa. c3 = hind coxa. s3 = metasternum. tr2 = mid trochanter

The erect dorsal bristles on the wing and scutellum in the subgenus *Neurochaeta* are probably important tactile organs when the insect moves under a low ceiling. There is a similarity here to suberect apical scutellar bristles of the genus *Nemo* (family Aulacigastridae, see McAlpine, 1983). At least some species of *Nemo* shelter under bark, a habitat which provides a low ceiling.

The plant association is unknown for *Neurochaeta sabroskyi*, but its proportions suggest a slightly different direction of specialization from that of related species. It seems probable that it is a sister species to *N. parviceps*, and out-group comparison both for the species pair and the collective group tends to confirm its derivation from broadly depressed forms. Yet *N. sabroskyi* has a much more slender body and wings. Although the fore coxae somewhat resemble those of *N. parviceps*, the pleural hollow is less marked, because narrowing of the mesoscutum allows less overhang of the pleural region. Hence we appear to have an adaptation pattern which has moved from wide, shallow crevices to something like pin-holes, or, more probably, when the accommodation of the legs is considered, in grooves which are both narrow and shallow.

APPEARANCE AND POSSIBLE MIMICRY

On exhibiting living material of *Neurochaeta* to laymen, a typical comment is something like: 'Are they flies? They look more like ants'. This reaction is presumably the result of several visible features. The size and slenderness of these insects are likely to be attributed to certain familiar domestic ants (e.g. species of genera *Iridomyrmex* and *Technomyrmex*) rather than to such familiar flies as domestic calliphorids and muscids. These attributes are, however, typical of numerous flies of the superfamily Asteioidea (in which Neurochaetidae are currently placed), and alone cannot be considered as evidence for mimicry of small ants by these flies. I shall consider some other characters which appear to support the view that some neurochaetids are Batesian mimics of small dolichoderine ants.

Adults of *Neurochaeta parviceps* and *N. inversa* have a general blackish body coloration relieved by a paler zone at the anterior end of the abdomen. The idea that this coloration may be of some adaptive significance receives support from the fact that it is emphasized by the pale sub-basal zone of the wings, when they are flexed over the abdomen, and also by the coloration of the halteres.

In *N. parviceps* and *N. inversa* in the subgenus *Neurochaeta* the halteres are bicoloured, with pedicels brownish and capitella creamy white. With the haltere directed posteriorly in the resting position, the dark pedicel lies against the dark posterior part of the thorax, and the whitish capitellum lies against the pale base of the abdomen. The wings being translucent, the coloration of the haltere reinforces the insect's longitudinal sequence of colour zones.

The coincidence of the distal parts of both wings over the abdomen gives the wings a low degree of visibility. The total impression, then, is of a slender, dark, wingless insect with a posterior part or gaster somewhat separated from the rest of the body, i.e. the appearance of a dark-coloured dolichoderine worker ant about 3 mm in length.

Comparison of *Neurochaeta* species with temperate Australian species of the micropezid genus *Metopochetus* tends to convince me that wing pattern in both is an element of Batesian mimicry of ants. *Metopochetus* species of the taxonomically unelucidated *M. terminalis* (Walker) complex are almost certainly mimics of ants of the genus *Leptomyrmex* (see Colless and McAlpine, 1970: fig. 34.29A, where incorrectly given as *M. tenuipes*). The larger *Metopochetus compressus* (Walker) is probably a mimic of aggressive stinging ants of the genus *Myrmecia*. These micropezid species have a complex wing pattern reinforced by superposition of the wings over the abdomen when at rest. The wings thus visually tend to lose their identity and give the impression of a basally narrowed, segmented abdomen. A closely related undescribed species of *Metopochetus* from Lord Howe Island has no wing pigmentation. Apparently there are no suitable ants to serve as models on this oceanic island. Several other micropezids, e.g. *Mimegralla contingens* (Walker) in northern Australia, New Guinea etc. and *Taeniaptera* spp. in Brazil, have a wing pattern similar to that of *Metopochetus* spp., though not closely related. Again I believe this convergence in pattern is best explained as due to ant-mimicry.

Neurochaeta species (e.g. *N. inversa*, see McAlpine, 1978: fig. 3) have a simpler wing pattern than the ant-mimicking *Metopochetus* species, probably because the smaller size of the former renders detailed representation of abdominal segmentation unnecessary.

Whether or not one is convinced of my theory of ant mimicry by *Neurochaeta* species, the evidence that colour pattern in these insects is adaptive is strongly supported by the fact that colour pattern of different parts of the insect is co-ordinated not only in such species as *Neurochaeta parviceps* and *N. inversa* as explained above, but also in other species with different schemes of coloration. *N. sabroskyi* has the capitellum of the haltere tawny, unlike other species of the genus, and also an almost uniformly brown-tinged wing membrane, and the anterior abdominal tergites brownish. *N. macalpinei*, on the other hand, has larger pale areas on the body than other species, paler legs, paler bristles, entirely creamy white halteres, and a larger pale sub-basal wing zone. The co-ordination of colour in wing, haltere and abdomen is apparent, and there is a possibility (but at present no evidence) that this species is a mimic of a small pale-coloured ant. In collecting the type series of *N. macalpinei*, Clyne and Frazier obtained, in association with the flies, a bug of the heteropterous family Anthocoridae. This is of similar size and coloration to the flies and could be a mimic of the same ant mimicked by them or even a mimic of the flies themselves. There is also a possibility that it is a predator of *Neurochaeta*.

The zigzag movements of *Neurochaeta* spp. are not particularly ant-like, though ants often do run quickly. This movement could, however, serve to display and reinforce the ant-like signal already learned by the predator.

A further feature observed in *Neurochaeta parviceps* and *N. inversa*, which is unusual for the higher Diptera and which increases resemblance to an ant, is the prognathous position of the head due to dorsal flexion at the neck in the living insect. The apparently short, high head of dried material is not ant-like, by comparison. The upward tilting of the head has been interpreted above as possibly aiding vision in a posterior direction, but I see no reason why it may not also aid in protective mimicry.

Ants, including small dolichoderines, have relatively long conspicuous antennae. Neurochaetids have not been observed to compensate visually for this lack by an appropriate position or motion of the fore legs, as has been observed in a number of dipterous mimics of Hymenoptera (McAlpine, 1973: 9-10). On the other hand, general impression rather than precision of detail is probably more important in mimics of such small size.

Mimicry of ants by other insects and spiders is a common and well established phenomenon (Wickler, 1968; author's numerous observations, and numerous other references in literature). It has occasionally been doubted that ants are suitable models for Batesian mimicry because they are preyed upon heavily by insectivorous vertebrates, the predators through which visual selection is most likely to operate. On the other hand I believe it probable that ants which contain acrid chemicals are likely to bring about predator satiation at relatively low levels of predation, at least in non-specialist predators. The fact that ant numbers are often very large increases both the probability of predator satiation and the probability that the predator will learn the visual signal. Ants with such a powerful sting as *Myrmecia* naturally produce a cautious approach in an experienced predator, which is likely to increase the chance of escape for a mimic.

It is interesting to note that the Baltic amber fossil neurochaetid *Anthoclusia gephyrea* Hennig (1965: fig. 244) has a wing pattern somewhat resembling that of *Neurochaeta inversa*. This suggests the possibility that neurochaetids have been mimics of ants for as long as 40 million years.

ADULT LONGEVITY

From what is known of the life-cycle of *Neurochaeta inversa* in New South Wales, over-wintering female adults would need to live for about 6 months in order to find an oviposition site and may in fact live even longer. Over-wintering males seem to live about as long as females, from my observations, and mating appears not to take place till an oviposition site is available (see McAlpine, 1978). Though I am not aware of any longevity experiments for such small flies in the field, it is probable that *N. inversa* adults have rather exceptional longevity for their size class. Perhaps such behavioural peculiarities as the extreme agility in running, the tendency to seek shelter, the devices which protect the wings from battering, the infrequent use of flight, and ingestion of such protein-rich food as pollen are adaptations to prolonged survival. It would be interesting to compare longevity, behaviour, and relation to the seasonal cycles of the host plants of the equatorial Malaysian species with those of *N. inversa*.

SPECIALIZATION AND REDUCTION OF OPTIONS

As usual in cases of extreme specialization, the locomotory behaviour in *Neurochaeta* seems to have narrowed the range of biological options. Thus fast running is carried out almost exclusively with a strong forward or backward component, and, for reasons still unexplained, the insect is unable to remain in any position except that with the body axis vertical while on a vertical surface. It is possible that even this restriction on orientation is adaptive, as discussed below.

The elongate body in *N. inversa* appears to be remarkably rigid. When the insect feeds from a leaf surface, the head is not flexed from the neck, but the body remains straight as its anterior end is sloped towards the substrate.

Observation on a captive specimen of *N. parviceps* indicated a restriction in locomotion due to rigidity of the body. The insect was placed in a stoppered cylindrical glass specimen tube *c.* 25mm by 50mm. The tube was inverted to give the container a glass ceiling. As expected, the insect ran up and down on the vertical glass wall with the body vertical and the head downwards. It repeatedly ran against the glass ceiling but each time it ran down again after contact. It was apparently unable to cross over the junction of the two surfaces at right angles to one another, and was reluctant to turn the body to make this transition possible. Eventually, after much contact with the ceiling, the body was turned horizontally and the transition to the ceiling readily made by walking sideways. Clearly inability to bend the body adequately, perhaps combined with shortness of the mid legs, prevented passing from the vertical to the horizontal surface when starting from the normal vertical body-position. No such difficulty existed for the insect in passing back from the ceiling to the wall, because, on the horizontal ceiling, there was no tendency towards a constant orientation of the body which could have prevented it approaching side-on to the vertical wall.

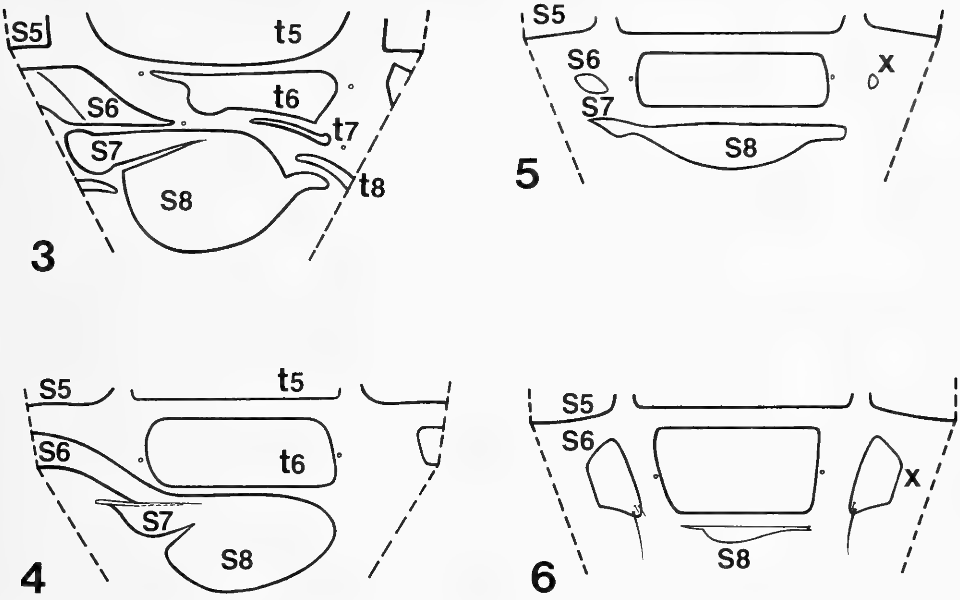
It is doubtful if the artificial situation just described simulates any frequently encountered natural situation. Flies on more mature inflorescences than those observed by us would frequently encounter the almost horizontal upper margins of bracts, and passing over this margin directly from the outer to the inner surface could pose a problem similar to that just described. One would expect, however, that any frequent, naturally occurring situation would not provide such difficulties in problem-solving. Field observations of *N. parviceps* in these situations would be interesting.

WHY UPSIDE-DOWN?

Given the advantages which may be conferred by the habit of running rapidly backwards and forwards in zigzags, the question remains as to why this habit has evolved in association with a head-down instead of an unrestricted or head-up orientation of the body.

It has been noted above that *Neurochaeta* species (and also *Nothoasteia* species) show apparent adaptations for running backwards, that these modifications are not uniform throughout the Neurochaetidae, and that the neurochaetid body-plan, like that of other Diptera, is primarily adapted for forward movement. In particular the eyes and other important sense-organs, which provide information as to conditions likely to be encountered during locomotion, are located on the head. It seems advantageous, then, for the neurochaetid fly to orient itself with the head pointing in the direction in which obstacles or dangers are most likely to be found. The cavities in which these flies shelter, e.g. the axils of bracts and hollowed petioles, and the spathal cavity of *Alocasia*, all open upwards, their closed lower ends forming an obstacle which, on repeated contact would eventually damage the wings. In the special case of phytotelmata, the opening is always upwards, and it would seem safest to approach the liquid surface, a potential sticky trap, head first. I have often noticed how moisture drops in glass vials tend to trap small flies by the wings. Thus, running wings-first towards the liquid surface could be particularly dangerous.

Some likely predators of *Neurochaeta* such as scincid lizards and frogs shelter in plant axils. Therefore running downwards into an axil head-first would seem more advantageous for flies than the reverse. Facing downwards while resting within the cavity does not, however, seem an advantageous position for watching for predators, and the neurochaetid habit of emerging from shelter backwards seems incautious. There is, however, a degree of rear vision and emerging backwards may not be particularly risky. The running is likely to be rapid and, as usual, evasive during emergence. A predator would need to be watching a particular axil carefully to be able to take advantage of a backward emergence.



Figs 3-6. Protandrograms of schizophorous Diptera, showing segments in front of male genital segment as if split along median ventral line and spread flat. 3. *Coelopa frigida* (Fabricius).. 4. *Neurochaeta prisca* (reconstructed from notes and sketches). 5. *N. capilo.* 6. *N. magnifica.* s5-s8 = sternites 5-8. t5-t8 = tergites 5-8. x = supernumerary sclerite.

It is interesting to note that flies of the genus *Stenomicra* (family Periscelididae or Stenomicridae), which often share the habitat of *Neurochaeta* species and are probably also associated with phytotelmata, maintain a consistent head-upwards orientation. But *Stenomicra* are not known to shelter in axils, they run less rapidly than the observed *Neurochaeta* species, and they do not move backwards and forwards in a zigzag path (McAlpine, 1978).

I postulate that the head-downwards orientation in the Neurochaetidae evolved during the early stages of development of zigzag running. In view of apparent adaptations for running backwards in *Nothoasteia*, this kind of orientation may be expected to occur in all known living neurochaetids, and possibly occurred in the forms known from fossils. But it is conceivable that this orientation did not become rigidly stereotyped, as in the subgenus *Neurochaeta*, until the flies acquired habitat preferences which brought them into frequent contact with phytotelmata.

DIVERSITY IN MALE POSTABDOMINAL STRUCTURES

The few known species of the genus *Neurochaeta* show a great diversity of structure in the segments behind segment 5 of the male abdomen. The male is unknown in subgenus *Neurotexis*.

Variation in sternites 6-8 consists of degree of reduction of these sclerites. Sternites 6 and 7 are well developed in *Neurochaeta* (*Neurocytta*) *prisca* (Fig. 4), where they are strongly asymmetrically placed. In this form the dorsal sternite 8 is also well developed. Subgenus *Neurocytta* thus has the most plesiomorphic condition of these sternites known in the genus, as may be seen from the resemblance to the primitive schizophoran *Coelopa* (Fig. 3).

The remaining known species of the genus (subgenus *Neurochaeta*) show a trend towards reduction of sternites 6-8 and towards symmetry of these segments. *N. capilo* (Fig. 5) has sternites 6 and 7 much reduced but still discernible on the left side, while sternite 8 remains large and setulose. *N. macalpinei* and *N. parviceps* have these segments externally approximately symmetrical with a small sclerite below *each* lateral margin of tergite 6, and sternite 8 reduced to a narrow glabrous transverse strip. *N. inversa* resembles the above species in the symmetry of segment 6 but sternite 8 is absent. I previously (McAlpine, 1978) interpreted a dorsal sclerite of *N. inversa* as probably sternite 8, but comparison with other species of the subgenus not then available, indicates that the sclerite in question is the epandrium.

The protandrial structure of *Neurochaeta magnifica* is of special interest, most of its characters being strongly apomorphic. In contrast with that of other species of subgenus *Neurochaeta*, tergite 6, though unreduced, is asymmetrical, as is the reduced sternite 8. Ventrally segment 6 bears a symmetrical pair of lateral plates, each separated from the tergite by the pleural membrane as is the sternite of the previous segment. Each plate bears macrotrichia which are better developed than those of sternite 5. Were the phylogenetic derivation of *N. magnifica* not reasonably clear, one would probably interpret this structure as the result of median desclerotization of a large, primarily symmetrical sternite 6 resembling the preabdominal sternites (Fig. 6). However, the apparent facts that the *inversa* group is the sister group of the *magnifica* group, that these together form the sister group of the *parviceps* group, and that the three above groups together form the sister group of the *capilo* group, render such an interpretation implausible. The series of protandrograms (Figs 3-6) illustrates the direction of evolution of these structures in the genus *Neurochaeta*. Only the left ventral sclerite of segment 6 in *N. magnifica* can be the homologue of sternite 6, its mirror image on the right side being a secondary sclerite. This condition is somewhat paralleled in *Fannia* (Griffiths, 1972) and *Borboroides* (McAlpine, 1985), where structures present only on the left side in the ancestral form have been mirrored by new structures on the right side, with resultant symmetry. In *N. magnifica*, however, it appears that evolution of segment 6 is in the process of incorporation into the preabdomen, as a continuation of the sclerotization process would restore a full, symmetrical sclerite simulating a typical preabdominal sternite. This kind of process may well be the clue to the possession of an apparent symmetrical, ventral sternite 6 in males of such flies as *Waterhouseia* (family Heleomyzidae, see McAlpine, 1985). It has long appeared to me from study of other families that the groundplan condition of the Schizophora includes strongly asymmetrical protandrial sclerites as in Coelopidae (Crampton, 1942: fig. 12H), and that symmetrical conditions of the protandrium are all secondarily derived. As protandrial morphology has figured prominently in arguments on phylogeny and superfamily classification (see particularly Griffiths, 1972), the correct evolutionary interpretation is important.

Some aspects of the functional changes in the evolution of the neurochaetid protandrium are easily explained. The asymmetry of the sclerites was apparently attained in a remote Mesozoic ancestor through spiral displacement in the process of circumversion of the genital segment (Crampton, 1942). This spiral arrangement of the tergites and sternites in segments 5 to 8 is preserved in modern Coelopidae with almost diagrammatic clarity (Fig. 3). With slight modification, this pattern occurs in the plesiomorphic neurochaetid *Neurochaeta* (*Neurocytta*) *prisca*. *N. prisca* is a relatively large neurochaetid, and size in the groundplan of subgenus *Neurochaeta* had probably been reduced to no more than about 3 mm total length as exemplified by 5 of the 6 known species. Size reduction in flies, as in other animals, is often accompanied by structural simplification, possibly because of ontogenetic difficulties in producing a diversity of structures from small materials, or perhaps mainly because a smaller organism can function on a simplified plan more readily than can a larger organism. In particular, a smaller body requires less skeletal support. In any case the subgenus *Neurochaeta* has developed a tendency towards symmetry by reduction, *N. capilo* (Fig. 5) and *N. parviceps* showing different stages of this process. Apart from the size reduction-simplification factor, the inherent instability in copulatory structures resulting from speciation processes, considered below, combined with the mechanical requirements of approximate symmetry in flight, are factors which should contribute to development of symmetry. The increase in body size and consequent need for skeletal support, and for a base for additional sensory macrotrichia in *N. magnifica* has resulted in increased ventral sclerotization of segment 6. But in this case there has been no tendency for this reversal of selection pressure to restore the lost asymmetrical sclerites, and resclerotization of the region has produced a new almost symmetrical pattern.

In *N. prisca* the epandrium is well developed and the surstyli are loosely articulated with its margins. In the species of subgenus *Neurochaeta* the surstyli are detached from the reduced epandrium and arise each from its separate basal plate.

The gonites (paired appendages of the hypandrium) consist of a single pair in *N. prisca* and two pairs in subgenus *Neurochaeta*. Like the surstyli they show specific differences in shape.

The aedeagus shows considerable specific variation in length, thickness, and armature in the genus *Neurochaeta*.

Specific differences in male copulatory organs occur in most families of Diptera, sometimes being more remarkable than in the examples cited above, e.g. those in the aedeagus of the heleomyzid genus *Diplogeomyza* (McAlpine, 1967). The Diptera are not peculiar in this respect as such specific characters are so general in insects that taxonomic work on most orders normally takes these characters into account. Probably for insect groups in general it may be stated that the male copulatory organs are more consistently than any other organs the ones which show morphological divergence between closely related species. There is a parallel here with acoustical behaviour, though the latter is probably of less wide occurrence among insects.

Highly specific genitalia characters occur in other groups of animals besides insects. They have been described in many Acari (e.g. Davis, 1968), in Diplopoda (e.g. Johns, 1964), in monogenetic trematodes (Sproston, 1946), in gastropods (e.g. Solem, 1981), in snakes (Dowling and Savage, 1960), in carnivorous marsupials (Woolley, 1982), and in rodents (e.g. Lidicker, 1968). These are probably all cases where there is or has been a possibility of the sexual stages of related species mixing with one another.

There has been difference of opinion as to the reason for specific diversity in the genitalia of insects. Some have held that these specific differences constitute a 'lock and key' isolating mechanism (e.g. Watson, 1966). Mayr (1963: 104), while admitting that mechanical isolation (e.g. by means of genitalia difference) plays 'a very minor role', explains this diversity as neither adaptive nor contributing to isolation, but as a side effect of pleiotropic genes.

SPECIFIC MATING MECHANISMS

Previously (McAlpine, 1969) I have classified specific difference in genitalia as an element of a '*specific mating mechanism*' rather than an isolating mechanism. A specific mating mechanism is defined as any genetically based device which tends to prevent mating or attempted cross-fertilization between species. Common specific mating mechanisms among insects include specific differences in time or place of courtship, differences of courtship pattern, visible appearance, chemical secretion, song, or tactile recognition marks, and the necessarily correlated specific responses to the stimuli imposed by these.

Specific mating mechanisms have often been classed as 'premating isolating mechanisms' or interpreteted as 'reinforcement' of isolation through selection. They are, however, distinct from true isolating mechanisms, in that they are the result of, not necessarily the cause of, some degree of isolation between species, and the 'species isolation concept' is at best a misnomer. Their magnitude, complexity, and intraspecific constancy is only to be explained through their role as specific recognition marks, conditioned through inviability or inferior fitness (including heterozygote disadvantage) of the hybrids which they tend to eliminate. Inferior hybrid fitness is the true cause of isolation (McAlpine, 1969). It is pointed out that even mechanisms of low efficiency can be produced by natural selection, and that in nature hybrids can occur between species having well developed specific mating mechanisms. However, the combined effects of specific mating mechanisms can amount to almost 100% efficiency. Many pairs of species which hybridize readily in the laboratory rarely, if ever do so in nature, even when they are sympatric (Mayr, 1963; Bock, 1984).

In a study of acoustical behaviour in the so-called races of the *Drosophila paulistorum* complex, Bennet-Clark and Ewing (1970) found evidence suggesting that the original barrier to interbreeding is not a difference in song, which is only a secondary mechanism. The fact that sterility barriers are evolving with or even preceding differentiation of song illustrates my point that such specific mating mechanisms are not the real cause of isolation.

The clear distinction between isolation and the specific mating mechanism can be seen in the following example from literature. Fisher (1958) cites recurrent hybrids between the butterflies *Limenitis arthemis* and *L. astyanax* occurring at low frequency in the narrow zone of overlap of these two species. A strong mating preference (specific mating mechanisms on my understanding) is said to be responsible for this low frequency. Apparently the hybrid lineages are eliminated after a few generations because of inferior fitness. If Fisher's data are accurate, the gene pools of the two species are as effectively isolated as if every hybrid zygote perished. He is therefore mistaken in suggesting the populations to be subspecies rather than species. I would agree with Fisher that the 'sexual preference' is favoured by a selective process, but not that this process 'would establish an effective isolation', as effectively complete isolation continues even when the 'sexual preference' breaks down, though with some waste of activity and gametes.

In a reasonably stable population the genes of the overall genotype tend to make up a highly integrated set, and it has long been known that introduction of chromosomal material of one race into that of another can cause significant changes in fitness to the carriers of the mixed genotype (e.g. Dobzhansky and Spassky, 1944). In the case of sympatric interfertile incipient species (which have recently acquired sympatry or are the products of disruptive selection) the hybrid genotypes very generally have inferior fitness to the parental genotypes, or the parental populations will tend to lose their identities. Hence, selection for a specific mating mechanism can occur through interaction with a related species even if the hybrids are viable and fertile.

Thomas (1950) has described the intimate association of the male genital appendages with the vaginal opening of the female during copulation in *Sarcophaga* (Diptera, Sarcophagidae). In this genus the form of the external genitalia shows a high degree of variability which is quite specific, and the female is known to exercise a very precise choice on males attempting to copulate. The conclusion seems inescapable that the pattern of stimulation caused by the structure and perhaps the movements of the male genitalia assist the female to make this choice.

The various male postabdominal organs which show great variation in the genus *Neurochaeta* seem likely to affect the process of copulation in some way, so that a specific response is possible in the female. The large asymmetrically placed sternites 6 and 7 in subgenus *Neurocytta*, absent in subgenus *Neurochaeta*, seem likely to affect the articulation of the genital segment with the preabdomen and thus the mode of wielding the copulatory organs. The paired periphallic appendages, surstyli and gonites, most probably convey tactile stimuli to the female. There can be no doubt that the great difference in length of the aedeagus, together with difference in its cuticular armature between *N. capilo* and *N. parviceps*, enables specific discrimination by females, should any premating behavioural mechanism break down. Though adults of these two species are usually separated by host-plant preference, they can occasionally occur on the same plant.

Despite the views of Eberhard (1985) I find in male genitalia characters some evidence of the geographical character dislacement pattern dependent on patterns of sympatry. In the genus *Pseudopomyza* s.l. (Diptera, Pseudopomyzidae) the species occurring in Europe and that in Australia, each widely geographically isolated from others of the genus (probably for a very long period) and not very closely related to each other, have the surstyli essentially similar in shape. In New Zealand, where there are several species which must have evolved with some degree of contact with one another (Harrison, 1959) the surstyli show strong specific differences in shape from those of the above species and from each other. A similar pattern occurs in the genus *Australimyza* (Diptera, Carnidae), where the several New Zealand species have highly specific shapes for the surstyli, but the two species, which are geographically remote from others of the genus, in Australia and Macquarie Island respectively, have similar and relatively simple surstyli. Again, these last two do not appear closely related on the basis of other characters.

In flies of the genus *Euprosopia* and in some other genera of Platystomatidae there is a sclerotized, capsule-like segment of the aedeagus or penis called the glans which is inserted deeply into the female genital tract in copulation. The glans often differs in size between closely related species but is of remarkably constant size within a species, despite great individual variation in body size. In Queensland, the two partially sympatric species *E. separata* and *E. comes* are so similar that females are difficult to distinguish, but males are distinguishable by the size of the glans and some other secondary sexual characters (some information in McAlpine, 1973a). In the more southern part of its range, where it is the only species of its group, *E. comes* apparently has a glans intermediate in size between that of *E. separata* and the more northern populations of *E. comes*. Despite such examples as this I find a detailed uniformity in genitalia characters over a considerable geographic range to be usual in the dipterous groups I have studied.

These data seem to conflict with the pattern given by Eberhard (1985: chapter 3). In some, but not all, of Eberhard's cases the genitalic difference between allopatrics concerns species within genera of considerable specific diversity and the species compared are not necessarily very closely related. Again he may have too readily dismissed the likely significance of unknown historical patterns which could often have been quite complex. The existing allopatry often may be irrelevant to the speciation process. On the other hand some of Eberhard's arguments seem to presuppose that only coexistence of very closely related species can possibly be invoked as producing sexual selection for divergence *per se*, whereas copulations and sometimes hybridism in nature between species of a higher order of differentiation have been observed (e.g. in butterflies and birds).

I summarize my conclusions on specific mating mechanisms (SMMs) in the following 5 statements: —

1. SMMs arise through natural selection acting on sympatric populations of related species.
2. Production of SMMs is not part of the speciation process, though it commonly follows speciation.
3. SMMs reduce wastage of gametes and of time and energy in fruitless reproductive behaviour.
4. SMMs do not (in the long term) prevent introgression (do not cause isolation).
5. SMMs are probably generally maintained by selection.

It is now necessary to consider hypotheses which are not compatible with the SMM viewpoint, but which have arisen partly through some shortcomings of the isolation-reinforcement concept.

H. E. H. Paterson has often stated the view that, while recognition marks are stabilized within a species by natural selection, natural selection has not caused divergence in these characters between related sympatric species (the concept of the specific-mate recognition system or SMRS, see Lambert and Paterson, 1984). According to that viewpoint, divergence in characters involving recognition occurs as a result of random genetic changes in populations of small size before speciation. While the small population model of speciation has become widely accepted, taken alone it is quite incapable of explaining the widespread (in some groups quite general) phenomenon of much greater specific divergence in premating signals than in other characters. Mate recognition would still be an important stabilizing factor at the small population stage, though under reduced mate-choice some slightly deviant phenotypes may be accepted. As with the older speciation model based on geographic variation, an initiation of signal divergence could result, but in my view, there is no reason why, under allopatry, divergence in signal should vastly outstrip divergence in other characters. This final result is clearly directed, not random, and almost certainly depends on sympatry (some examples in genitalia characters given by McAlpine, 1969).

Paterson (1978) supports his view, that the reinforcement model (thus also the specific-mating model) cannot be evolved through interaction between incipient species, by a simple mathematical demonstration. This idea, that, if there is random mating and heterozygote disadvantage in a mixture of two genotypes, the rarer genotype will be so often absorbed into unfit heterozygotes that its extinction is assured, is valid under certain ideal circumstances (experiments of Harper and Lambert, 1983), but let us compare these requirements with the situation in nature.

First, why is it necessary to assume random mating? Paterson accepts that evolution after allpatric separation of a small population makes some divergence in 'SMRS' possible, and thus mating choice in subsequent sympatry need not be entirely random. It has been argued, however, that, where behavioural differences occur, they cannot alone prevent the extinction of one genotype in a closed system. Second, the development of 'reinforcement' or specific mating mechanisms occurs between populations that have diverged to the point of speciation, not between simple mutants of the one population. Third, and perhaps most important, the model depends on a nice mixing under closed conditions of the two genotypes, as in the few laboratory experiments which Paterson considers ideal. In nature the patchiness of the environment renders it more likely that there would be frequent invasion and possibly return between strongholds of the two population types. After each invasion the original occupier would have lost some material from the gene pool, preferentially that most likely to have facilitated cross mating. Any retreating invader would be similarly changed. The very experiments which have been rejected as irrelevant, those in which a mixed culture was artificially maintained, are those most likely to simulate a natural event. It has been pointed out that these laboratory experiments do not result in permanent fixation of mate recognition systems in the populations, but this is scarcely surprising. The established systems or mechanisms in natural species have often been evolved over many thousands of years, and even then may be imperfect enough to allow occasional hybrids, e.g. in birds of paradise (Gilliard, 1969) and birdwing butterflies (McAlpine, 1970), both groups with obvious specific recognition marks. There is reason to believe that, in sympatric sister species, specific mating mechanisms are maintained by selection, just as they were built up by selection. When changes in the environment bring about breakdown in the true isolating mechanism of hybrid inferiority, the species tend to fuse, because the specific mating mechanism can no longer be maintained (several examples given by Mayr, 1963: chapter 6).

It is not quite reasonable of Lambert and Paterson (1984), whenever there is geographic variation in signal characters, to claim that this variation cannot be in those characteristics of the signal that involve recognition. If the observed variation does not involve recognition marks, why else should it follow the geographic character-displacement pattern observed, for instance, by Littlejohn (1965)? Littlejohn's explanation fits the observed facts, but the SMRS school provides no adequate explanation of observed phenomena. On the other hand, the positive aspect of the SMRS argument does explain the remarkable consistency of specific mating mechanisms within a species, which may extend throughout its geographic range if gene flow permits.

Certainly, some of my above points have been considered by the anti-reinforcement school. For example, Harper and Lambert (1983) consider the effect of continued immigration of one species, but argue that continued gene flow (i.e. introgression) would probably prevent divergence of the populations. As I have previously pointed out, the divergent genomes (under the allopatric speciation model) need to have reached, prior to sympatry, a degree of divergence which ensures that each integrated genome has such superior fitness that hybrid lines are virtually certain to die out in the long term. Populations that have not so diverged are irrelevant to the speciation process, even though they may, if allopatric, be given separate specific names.

Eberhard (1985) discusses Fisher's concept of sexual selection by runaway female choice and favours this explanation for specific divergence in genitalia characters over selection for divergence under at least partial sympatry. Kirkpatrick (1982) has produced a mathematical model for this system. Eberhard argues that the other function of copulation (i.e. other than essential sperm transfer) 'is that of inducing females to receive and use sperm or, in a broad sense, courtship'. The tendency for females to be selective in their sexual partners is a well known corollary of the facts of production of different numbers of gametes and the making of different kinds of investment in the offspring by the two sexes. This principle is also significant in the specific mating mechanism concept. The runaway process can indeed be invoked to explain rapid change in these circumstances, but that the change is under a special kind of control is evidenced by the end result, viz. remarkable uniformity within a species and sharp interspecific difference. These almost universal phenonema do not necessarily arise as the consequence of 'runaway selection' as described particularly by Eberhard. The theoretical effects of this selection, especially under the explanations given by Eberhard (1985:72), should be a continuing instability and elaboration of detail through female choice favouring novel stimuli. Very generally, such instability does not occur in male genitalia characters. Amazingly, when Eberhard comes to consider intraspecific uniformity of genitalia as a stumbling block to his hypothesis (Eberhard, 1985: 151-153), he finds this evidence 'difficult to evaluate', and then all but denies its existence.

There is also a weakness in the converse side of the runaway female choice argument. Why, if the process takes place quite independently in each species, does it virtually always (in the relevant animal groups) result in strong divergence in genitalic characters? It might be expected that in the *more complex* systems change *per se* would *usually* result in divergence, but the divergence phenomenon is quite general for various levels of structural complexity.

Some further inconsistencies occur in Eberhard's arguments. He argues (a) that copulation is part of the courtship ritual (b) that copulation is not necessarily the final stage at which female choice can be exserted. (I can agree on both counts.) He then argues that the fact, that the poor correlation of simple, uniform (i.e. non-specific) male genitalia characters with (specific) elaborate premating behaviour, seriously weakens the species isolation hypothesis (presumably meaning for genitalia differences as distinct from courtship differences). As indicated elsewhere, I do not consider any one mechanism to be 100% efficient to the exclusion of other mechanisms; further there is no necessity in any case to believe that the premating mechanism was evolved before the genitalic one, and special problems in gamete wastage will favour reinforcement of recognition mechanisms at all stages in the sexual sequence.

Finally, there are many cases where closely related species do occur sympatrically, are interfertile, and occasionally produce hybrids. The fact that these hybrids (and not the parent species) are eliminated means that 'reinforcement' selection is certainly acting. I find it just about as surprising, then, that some biologists should attempt to disprove the existence of this selection process, as that they should attempt to disprove the existence of upside-down flies.

TAXONOMIC CHARACTERS AND ADAPTATION

The view that genetic changes which result in taxonomic characters are generally differentially adaptive is probably widely accepted. A taxonomic character, if genuine, is generally the phenotypic expression of a number of genes, though it may not represent the whole adaptive expression of any one of its causative genes. The theory of the adaptive nature of taxonomic difference is closely related to the specific niche theory. For both theories, support can be found in many specific examples, but a general proof is not available. Species divergence need not, however, depend on competition.

It is quite possible for taxonomic difference to be adaptive without its bearing on any ecological difference between taxa. Often a taxonomic difference is adaptive to the internal environment of an organism which has itself become modified for various historic and probably adaptive reasons. The difference in chaetotaxy (bristle pattern) between such flies as *Homoneura* (family Lauxaniidae) and *Leucophenga* (family Drosophilidae) may be of this kind. The existing pattern in each group is stable, apparently because it fits the very complex physiology of the organism, although mutations liable to cause different patterns are often produced. Drosophilids manage best without a mesopleural bristle; lauxaniids need a mesopleural bristle (except in the special case of the Celyphinae), though flies of the two groups seem to be performing the same things.

I have consistently sought Darwinian explanations for morphological change and divergence, because no established modern theory has been able to displace 'progressive adaptation' as the driving force in morphological evolution. Neither the theory of molecular drive (Dover, 1982) nor the neutral theory of molecular evolution (outlined by Kumura, 1985) is claimed to have much direct bearing on morphological change, though both are concerned with change at the molecular level. Sometimes, however, hypotheses regarding morphological developments of unknown function are put forward, and there can be a tendency to interpret these under the above categories.

Vines (1982), perhaps finding difficulty in explaining specific differences as the effects of selection, suggests that molecular drive may have an effect 'on any aspect of the phenotype, from sexual behaviour to morphology'. If this generalization is to be applied to the phenotypes here classed as specific mating mechanisms, then its protagonists must explain the curious coincidence that these phenotypes are always those which have the potential to enable specific discrimination in mating pairs.

Arrow (1951), discussing evolution of enlarged mandibles and horns in Coleoptera, infers a form of evolutionary momentum when he states 'because a process [of evolution] is long continued it is not easily discontinued'. Such ideas have been largely countered by responsible arguments (e.g. Otte and Stayman, 1979; Charlesworth, 1984). Recent interesting studies of evidence for function of diverse developments have included: stalked eyes in Diptera (McAlpine, 1979; Burkhardt and Motte, 1983), horns in Coleoptera (Otte and Stayman, 1979; Eberhard, 1979 — Arrow's problem!); horns in Diptera (Moulds, 1977); diverse secondary sexual developments in Diptera (elements of specific mating mechanisms, McAlpine, 1973b); shell geometry in gastropods (Signor, 1985); coloration in insects (a few examples and references in Matthews, 1976); stripes in zebras (Cloudsley-Thompson, 1984 — involving Diptera!); the tusk in male narwhals (Cetacea) (Gerson and Hickie, 1985). The last example provides support for the analogy I have drawn (McAlpine, 1976) between sinistrally spiral narwhal tusks and sinistrally spiral vibrissae in certain clusiid flies. The examples here quoted can be categorized with most of the morphological types sometimes considered inexplicable in terms of Darwinian selection. The need for alternative theories seems to be disappearing as we take a closer look at organisms in nature.

In the above discussion in general I have been using the term adaptation in virtually a traditional sense, but also in the special sense of Gould and Vrba (1982). That my interpretation of usage of the morphological developments should sometimes extend these characters into the category of exaptation (using the terminology of Gould and Vrba) is for the most part improbable and not intentional. This is because I am considering new developments, which are apomorphies in relation to the groundplan of the Asteioidea and often in relation to that of the Neurochaetidae or even of subgenus *Neurochaeta*. Hence the characters are not likely to be preadapted to uses other than those pertaining to the derived biological pattern of neurochaetids. The possible exception involves the prognathous position of the head in subgenus *Neurochaeta*, which appears to have dual usage in ant mimicry and rear vision. However, there is no reason to assume that prognathy preceded the early stages of either ant mimicry or running backwards and it may be a simultaneous adaptation to two functions.

Attempts by taxonomists to interpret in functional or adaptive terms the characters used in classification are occasionally made, mainly in the more obvious categories, such as specific diversity of bills of birds (examples in Tyne and Berger, 1959). In insects, with the enormous number of taxa and consequently of taxonomic characters, few taxonomists have given time to consider the functional aspects of the characters, and lack of relevant biological data has often placed the problem beyond profitable consideration.

Hlavac (1972) has given a morphological account of the prothorax of Coleoptera, relating the major structural types to locomotory mechanism and habitat adaptation. The differences in structure are to some extent the character differences for major taxa of Coleoptera. He finds that, at somewhat lower taxonomic levels convergence is common 'and putatively unique paradaptive features' are infrequent. This statement recalls the apparent convergence in characters relating to thoracic depression between *Nothoasteia* and the more advanced species of the *Neurochaeta* lineage.

Generation of morpho-adaptive hypotheses for the Neurochaetidae is simpler than for most families of Diptera, because of the small number of taxa, the fairly clear picture of part of the phylogeny (partly from reference to a key fossil), and some understanding of their biology.

In discussing the morphology of the Neurochaetidae I have produced a series of hypotheses as to adaptive values, which are in accord with the very limited available data on the biology of the insects, or which, considered in relation to one another, make up a plausible picture of aspects of the evolutionary adaptation of neurochaetid flies. In taking my deductions somewhat into the field of speculation I have proceeded further than is usual in the field of insect physiology, but not further than is commonly accepted in the fields of palaeontology and phylogenetic systematics, where elaborate hypotheses are often produced on evidence which is slight or liable to more than one interpretation. As in those fields, I believe that reasonable hypotheses on morphological adaptation in insects are a step towards a more complete understanding of a little investigated but highly complex subject, and provide some indications for the direction of future work.

ACKNOWLEDGEMENTS

I am indebted to W. D. Hamilton, R. W. Taylor and D. J. Bickel for discussion of some of the ideas here put forward. K. C. Khoo assisted in field observations, B. Duckworth assisted with the illustrations, and J. Howarth processed the words.

References

Arrow, G. J., 1951. — *Horned beetles, a study of the fantastic in nature.* The Hague: W. Junk.

Bennet-Clark, H. C., and Ewing, A. W., 1970. — The love song of the fruit fly. *Scientific Amer.* 223: 84-92.

Bock, I. R., 1984. — Interspecific hybridization in the genus *Drosophila. Evol. Biol.* 18: 41-70.

Boonsong, L., and McNeely, J. A., 1977. — *Mammals of Thailand.* Bangkok: Kurusapha Ladprao Press.

Burkhardt, D., and Motte, I. de la, 1983. — How stalk-eyed flies eye stalk-eyed flies: observations and measurements of the eyes of *Cyrtodiopsis whitei* (Diopsidae, Diptera). *J. Comp. Physiol.* 151: 407-421.

Charlesworth, B., 1984. — Evolution of the giraffe's neck. *New Scient.* 1426: 59-61.

Cloudsley-Thompson, J. L., 1984. — How the zebra got his stripes — new solutions to an old problem. *Biologist* 31: 226- 228.

Colless, D. H., and McAlpine, D. K., 1970. — Chapter 34. Diptera. In *The insects of Australia:* 656-740. Melbourne: Melbourne University Press.

Crampton, G. C., 1942. — The external morphology of the Diptera. *Bull. Conn. geol. nat. Hist. Surv.* 64: 10-165.

Davis, J. J., 1968. — Studies in Queensland Tetranychidae. 7. Records of the genus *Eotetranychus* (Acarina: Tetranychidae). *J. Aust. ent. Soc.* 7: 127-129.

Dobzhansky, T., and Spassky, B., 1944. — Genetics of natural populations. XI. Manifestation of genetic variants in *Drosophila pseudoobscura* in different environments. *Genetics* 20: 270-290.

Dover, G., 1982. — Molecular drive: a cohesive mode of species evolution. *Nature* 299: 111-117.

Dowling, H. G., and Savage, J. M., 1960. — A guide to the snake hemipenis: a survey of basic structure and systematic characteristics. *Zoologica* 45: 17-28, 3 pl.

Eberhard, W. G., 1979. — The function of horns in *Podischnus agenor* (Dynastinae) and other beetles. *In* M. S. and N. A. Blum, (eds), *Sexual selection and reproductive competition in insects:* 231-258. New York: Academic Press.

——, 1985. — *Sexual selection and animal genitalia.* Cambridge, Mass: Harvard University Press.

Fisher, R. A., 1958. — *Genetical theory of natural selection.* 2nd edition. New York: Dover.

Gerson, H. B., and Hickie, J. P., 1985. — Head scarring on male narwhals (*Monodon monoceros*); evidence for aggressive tusk use. *Can. J. Zool.* 63: 2083-2087.

Gilliard, E. T., 1969. — *Birds of paradise and bower birds.* London: Weidenfeld and Nicolson.

Gould, S. J., and Vrba, E. S., 1982. — Exaptation — a missing term in the science of form. *Paleobiol.* 8: 4-15.

Griffiths, G. C. D., 1972. — *The phylogenetic classification of Diptera Schizophora with special reference to the structure of the male postabdomen.* Hague: W. Junk.

Harper, A. A., and Lambert, D. M., 1983. — The population genetics of reinforcing selection. *Genetica* 62: 15-23.

Hennig, W., 1965. — Die Acalyptratae des Baltischen Bernsteins und ihre Bedeutung für die Erforschung der phylogenetischen Entwicklung dieser Diptera-Gruppe. *Stuttgart. Beitr. Naturk.* 145: 215 pp.

Hlavac, T. J., 1972. — The prothorax of Coleoptera: origin, major features of variation. *Psyche* 79: 123-149.

JOHNS, P. M., 1964. — The Sphaerotrichopidae (Diplopoda) of New Zealand. 1. Introduction, revision of some known species and descriptions of new species. *Rec. Canterbury* (N.Z.) *Mus.* 8: 1-49.

KIMURA, M., 1985. — The neutral theory of molecular evolution. *New Scient.* 1464: 41-46.

KIRKPATRICK, M., 1982. — Sexual selection and the evolution of female choice. *Evolution* 36: 1-12.

LAMBERT, D. M., and PATERSON, H. E. H., 1984. — On 'bridging the gap between race and species': the isolation concept and an alternative. *Proc. Linn. Soc. N.S.W.* 107: 501-514.

LIDICKER, W. Z., 1968. — A phylogeny of New Guinea rodent genera based on phallic morphology. *J. Mammal.* 49: 609-643.

LITTLEJOHN, M. J., 1965. — Premating isolation in the *Hyla ewingi* complex (Anura: Hylidae). *Evolution* 19: 234-243.

MCALPINE, D. K., 1967. — The Australian species of *Diplogeomyza* and allied genera (Diptera, Heleomyzidae). *Proc. Linn. Soc. N.S.W.* 92: 74-106.

——, 1969. — Systematic studies in Australian Platystomatidae (Diptera). London: University of London, Ph.D. thesis, unpubl.

——, 1970. — A note on the status of *Ornithoptera allottei* (Rothschild) (Lepidoptera: Papilionidae). *J. Aust. ent. Soc.* 9: 233-234.

——, 1973a. — The Australian Platystomatidae (Diptera, Schizophora) with a revision of five genera. *Mem. Aust. Mus.* 15: 256 pp.

——, 1973b. — Observations on sexual behaviour in some Australian Platystomatidae (Diptera, Schizophora). *Rec. Aust. Mus.* 29: 1-10.

——, 1976. — Spiral vibrissae in some clusiid flies (Diptera, Schizophora). *Aust. ent. Mag.* 3: 75-78.

——, 1978. — Description and biology of a new genus of flies representing a new family (Diptera, Schizophora, Neurochaetidae). *Ann. Natal Mus.* 23: 273-295.

——, 1979. — Agonistic behaviour in *Achias australis* (Diptera, Platystomatidae) and the significance of eyestalks. *In* M. S. and N. A. BLUM, (eds) *Sexual selection and reproductive competition in insects:* 221-230. New York: Academic Press.

——, 1983. — A new subfamily of Aulacigastridae (Diptera: Schizophora), with a discussion of aulacigastrid classification. *Aust. J. Zool.* 31: 55-78.

——, 1985. — The Australian genera of Heleomyzidae (Diptera: Schizophora) and a reclassification of the family into tribes. *Rec. Aust. Mus.* 36: 203-251.

——, 1988. — Studies in upside-down flies (Diptera: Neurochaetidae). Part I. Systematics and phylogeny. *Proc. Linn. Soc. N.S.W.* 110: 31-58.

MATTHEWS, E. G., 1976. — *Insect ecology.* St Lucia, Qd: University of Queensland Press.

MAYR, E., 1963. — *Animal species and evolution.* Cambridge, Mass: Harvard University Press.

MOULDS, M. S., 1977. — Field observations on behaviour of a north Queensland species of *Phytalmia* (Diptera: Tephritidae). *J. Aust. ent. Soc.* 16: 347-352.

OTTE, D., and STAYMAN, K., 1979. — Beetle horns: some patterns of functional morphology. *In* M. S. and N. A. BLUM, eds, *Sexual selection and reproductive competition in insects:* 259-292. New York: Academic Press.

PATERSON, H. E. H., 1978. — More evidence against speciation by reinforcement. *S. Afr. J. Sci.* 74: 369-371.

SHAW, D. E., and CANTRELL, B. K., 1983. — Further notes on seed set in *Alocasia macrorrhiza* (Araceae) and occurrence of *Neurochaeta inversa* (Diptera: Neurochaetidae) in Queensland. *Qd Nat.* 24: 71-75.

——, ——, and HOUSTON, K. J., 1982. — *Neurochaeta inversa* McAlpine (Diptera: Neurochaetidae) and seed set in *Alocasia macrorrhiza* (L.) G. Don (Araceae) in southeast Queensland. *Proc. Linn. Soc. N.S.W.* 106: 67-82.

SIGNOR, P. W., 1985. — The role of shell geometry as a deterrent to predation in terebrid gastropods. *Sci. in N. Guinea* 11: 81-95.

SOLEM, A., 1981. — Camaenid land snails from Western and Central Australia (Mollusca: Pulmonata: Camaenidae). II. Taxa from the Kimberley, *Amplirhagada* Iredale, 1933. *Rec. West. Aust. Mus. Suppl.* 11: 147-320.

SPROSTON, N. G., 1946. — A synopsis of the monogenetic trematodes. *Trans zool. Soc. London* 25: 185-600.

STONE, B. C., 1982. — New Guinea Pandanaceae: first approach to ecology and biogeography. *In* J. L. GRESSITT, (ed.), *Biogeography and ecology of New Guinea* 1: 401-436.

THOMAS, H. T., 1950. — Field notes on the mating habits of *Sarcophaga* Meigen (Diptera). *Proc. Roy. ent. Soc.* (A) 25: 93-98.

TYNE, J. VAN, and BERGER, A. J., 1959. — *Fundamentals of ornithology.* New York: John Wiley and Sons.

VINES, G., 1982. — Molecular drive: a third force in evolution. *New Scient.* 96: 664-665.

WATSON, J. A. L., 1966. — Genital structure as an isolating mechanism in Odonata. *Proc . Roy. ent. soc. Lond.* (A) 41: 171-174.

WICKLER, W., 1968. — *Mimicry in plants and animals.* New York: McGraw-Hill.

WOODLEY, N. E. 1982. — Two new species of *Neurochaeta* McAlpine (Diptera: Neurochaetidae), with notes on cladistic relationships within the genus. *Mem. ent. Soc. Wash.* 10: 211-218.

WOOLLEY, P. A. 1982. — Phallic morphology of the Australian species of *Antechinus* (Dasyuridae, Marsupialia): a new taxonomic tool? *In* M. ARCHER, (ed.), *Carnivorous marsupials* 2: 767-781. Sydney: Royal Zoological Society of N.S.W.

A new Genus and four new Species in the Family Echinasteridae (Echinodermata: Asteroidea)

FRANCIS W. E. ROWE and E. LYNNE ALBERTSON

ROWE, FRANCIS W. E., & ALBERTSON, E. LYNNE. A new genus and four new species in the family Echinasteridae (Echinodermata: Asteroidea). *Proc. Linn. Soc. N.S.W.* 110 (1), (1987) 1988: 83-100.

A new genus and four new species of echinasterid asteroids are described. The species are recorded from South African, southern and southeastern Australian, Japanese and northwestern North American waters. The genus is characterized by the occurrence of a large, hyaline-tipped recurved spine at the apex of the jaw. The genus otherwise shows a close relationship with *Henricia* Gray (1840).

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INTRODUCTION

During an investigation of the echinoderm fauna of New South Wales, taxonomic problems became apparent in members of the asteroid spinulosid family Echinasteridae. The identity of species of the genus *Henricia* in southern and southeastern Australia and the description of a new species of *Echinaster* from New South Wales, have been reported by us elsewhere (Rowe and Albertson, 1987a, b).

The present taxonomic problem deals with a geographically widespread group of new species which share in common a large recurved hyaline-tipped spine at the apex of the jaw angle. All other features are typically echinasterid. The presence of this apical tooth was identified first amongst southern and southeastern Australian specimens identified in the genus *Henricia* held in the Australian Museum (AM) and Museum of Victoria (MV) collections. During a visit to the United States National Museum (USNM) the senior author found two additional specimens, one from Japanese waters, the other from off Washington State, NW coast of North America. Finally two specimens were included amongst a collection identified as *Henricia abyssalis* from South African waters, on loan from the British Museum (Natural History) (BM(NH))in London, U.K.

SYSTEMATIC DESCRIPTION

Family ECHINASTERIDAE Verrill (1867)

Genus ***Odontohenricia*** nov.

Description: An echinasterid sea star with 5 rays (rarely 6); reticulate abactinal skeleton, plates raised centrally forming ridges which bear spinelets; marginal series distinguishable, inferomarginal plates pronounced; papulae present abactinally, marginally and actinally; 2-3 furrow spines in vertical series; large recurved hyaline spine present at apex of each pair of oral plates, the size 3 to 4 times greater than adjacent spines.

Type species: *Odontohenricia endeavouri* n.sp., herein designated.

Etymology: *odontos* = (Greek) tooth, referring to the apical oral spine characterizing this genus.
henricia = named after the genus *Henricia*, in recognition of the otherwise close morphological association of these genera.

Other species included: *O. clarkae* n.sp., *O. fisheri* n.sp., *O. hayashii* n.sp.

Remarks: *Odontohenricia* differs from all other members of the family by possessing a recurved apical spine. Otherwise the new genus appears to share most features in common with *Henricia* Gray, 1840, including the form of skeleton and arrangement of spines.

Considering the general echinasterid features of these species, we do not believe the possession of this hyaline-tipped apical spine warrants the establishment of a new family. We do, however, consider this discrete group of species should be recognized within its own supra-specific taxon and describe a new genus accordingly. As far as we are aware, the recurved apical spine is a feature shared only with members of the valvatid family Odontasteridae.

Within the Echinasteridae, *Plectaster* Sladen, 1889 is the only genus in which the furrow spines occur in a comb-shaped row along the adradial edge of the adambulacral plate (Fig. 1). We believe this genus does not belong in this family, though we decline herein to reassign it, since it is outside the scope of this paper.

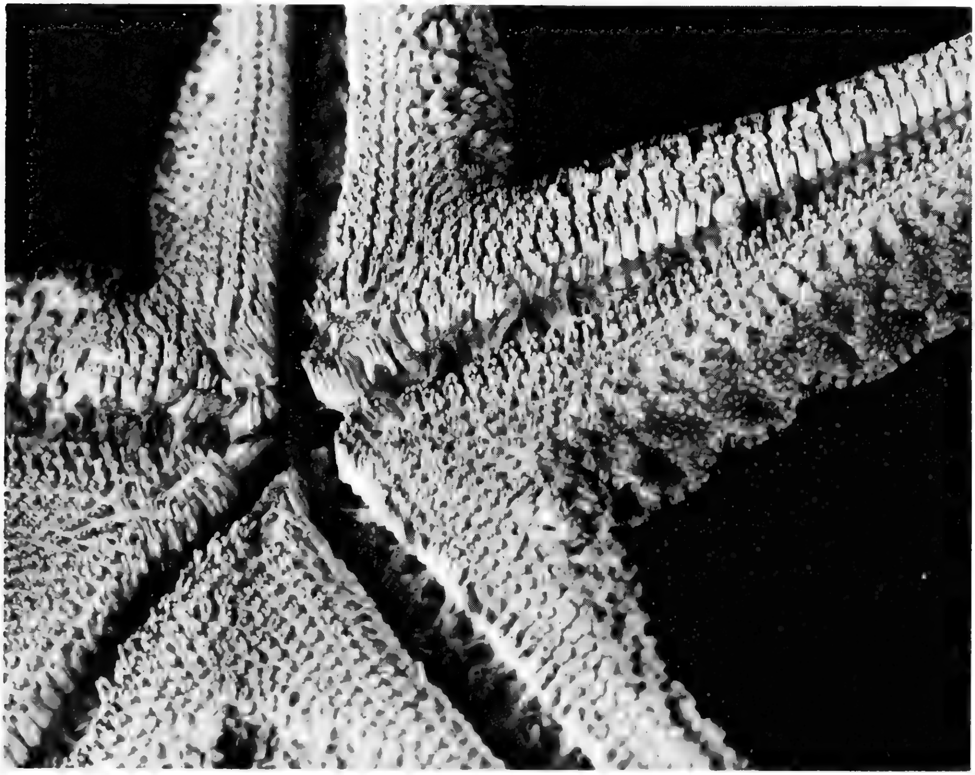

Fig. 1. Plectaster decanus (AM J13074): Actinal surface showing the comb-shaped rows of spines along the adradial edge of the adambulacral plates.

Odontohenricia endeavouri n.sp.
Figs 2**A-B**, 3**A-B**, 4**A-E**

Henricia hyadesi, H. L. Clark, 1916: 60 (part); 1946: 148 (part) [non *H. hyadesi* (Perrier, 1891) = *H. obesa* (Sladen, 1889) according to Fisher, 1940: 164].

Diagnosis: Rays 5, rarely 6, R=31-83mm, r=5-14mm, R/r=5-12, inflated proximally and tapering; abactinal skeleton closely reticulate, 1-2 rarely 3 papulae per papular area; plates overlapping, irregular, ovoid to stelloid form; plates medially ridged bearing fine spinelets which taper to an acute tip, spinelets in tufts of 3-9, or in 1-3 comb-like irregular rows; marginal plates distinct, ridged medially and bear spinelets, superomarginals and inferomarginals quadrilobed, inferomarginal plates markedly higher than wide, intermarginal plates more or less quadrilobed with small plates between, 1-3 series, actinal plates quadrilobed 1-3 series, marginal spinelets as for abactinal plates; papulae extend to actinal series with 1 papula per area; 2 (3) furrow spines in vertical series, adambulacral plates with a large cylindrical or slightly compressed subambulacral spine on the adradial edge, behind which stand a pair of shorter but similar spines. Smaller serrately tipped subambulacral spines, occur across the remaining surface of the adambulacral plate, (these often appear to be aligned in a double row); large recurved spine at apex of oral angle, 4-5 spines occur along furrow margin of oral plates, 3-4 spines occur on actinal surface of oral plates.

Materials examined: Holotype, AM J8792, off Eden, New South Wales; 1 paratype, AM J7156, Lakes Entrance, Vic.; 1 paratype, AM J5859, Bass Strait west of Babel Island, 128m; 4 paratypes, AM J20080, off Eden, N.S.W.; 1 paratype, AM J3072, Great Australian Bight, 146.3-219.5m; 4 paratypes, MV Acc. No 75-9, 38°44′S, 141°33′E, 18 miles south of Cape Nelson, Vic., 153.6m; 3 paratypes, MV Acc. No 75-9, 38°44′S, 141°33′E, 12.5 miles south of Cape Nelson, Vic., 146.3-155.4m; 1 specimen, AM J12868, 34°21′S, 151°24′E to 34°14′S, 151°28′E, northeast of Wollongong, N.S.W., 402m; 1 specimen, AM E3648, Great Australian Bight, 146-274m; 1 specimen, AM J5857, Bass Strait; 1 specimen, AM J17266, 34°43′S 151°12′E to 34°38′S 151°16′E, N.S.W., 457m; 1 specimen, AM E3772, Great Australian Bight, 274m; 2 specimens AM J20081, 35°02′S 151°06′E to 34°58′S 151°08′E, off Shoalhaven, N.S.W., 439-420m; 2 specimens, AM J20082, 34°28′S, 151°19′E, N.S.W., 412m; 1 specimen, AM J7155, off Eden, N.S.W.; 1 specimen, AM J12871, 35°44′S, 150°37′E, east of Brush Island, N.S.W., 384m; 1 specimen, AM J13202, 38°12′S 149°49′E to 38°11′S 149°53′E, southeast of Gabo Island, Vic., 439m; 1 specimen, AM J7007, off Newcastle, N.S.W.; 1 specimen, AM J20083, 36 miles south of Mt Cann, Vic., 205m; 1 specimen, AM J7052, off Eden, N.S.W.

Distribution: Southeastern Australia, from off Newcastle, New South Wales to Bass Strait and the Great Australian Bight, in depths ranging from 128-457m.

Etymology: Named for the Federal Fisheries Investigation ship 'Endeavour' from which extensive collections of southeastern and southern Australian fauna, including echinoderms, were made.

Description: The holotype has 5 rays, inflated proximally and tapering to a fairly acute tip, R=40mm, r=7mm, R/r=5.7. The disc is small. The madreporite is small and ridged, occurring interradially at about ½r.

The abactinal skeleton (Figs 2**A**, 4**A**) is stout and closely reticulated, with 1-2, rarely 3 papulae per mesh. The overlapping plates are irregular — ovoid to stellate in shape. Additional small plates and processes occasionally project from the main skeletal plates into the papular region. The plates are raised centrally into low ridges bearing spinelets in tufts of 3-9, or in 2-3 irregular crescentic rows (Fig. 4**B**). The spinelets are fine, serrated and taper to an acute tip (length: 0.24mm, width: 0.06mm).

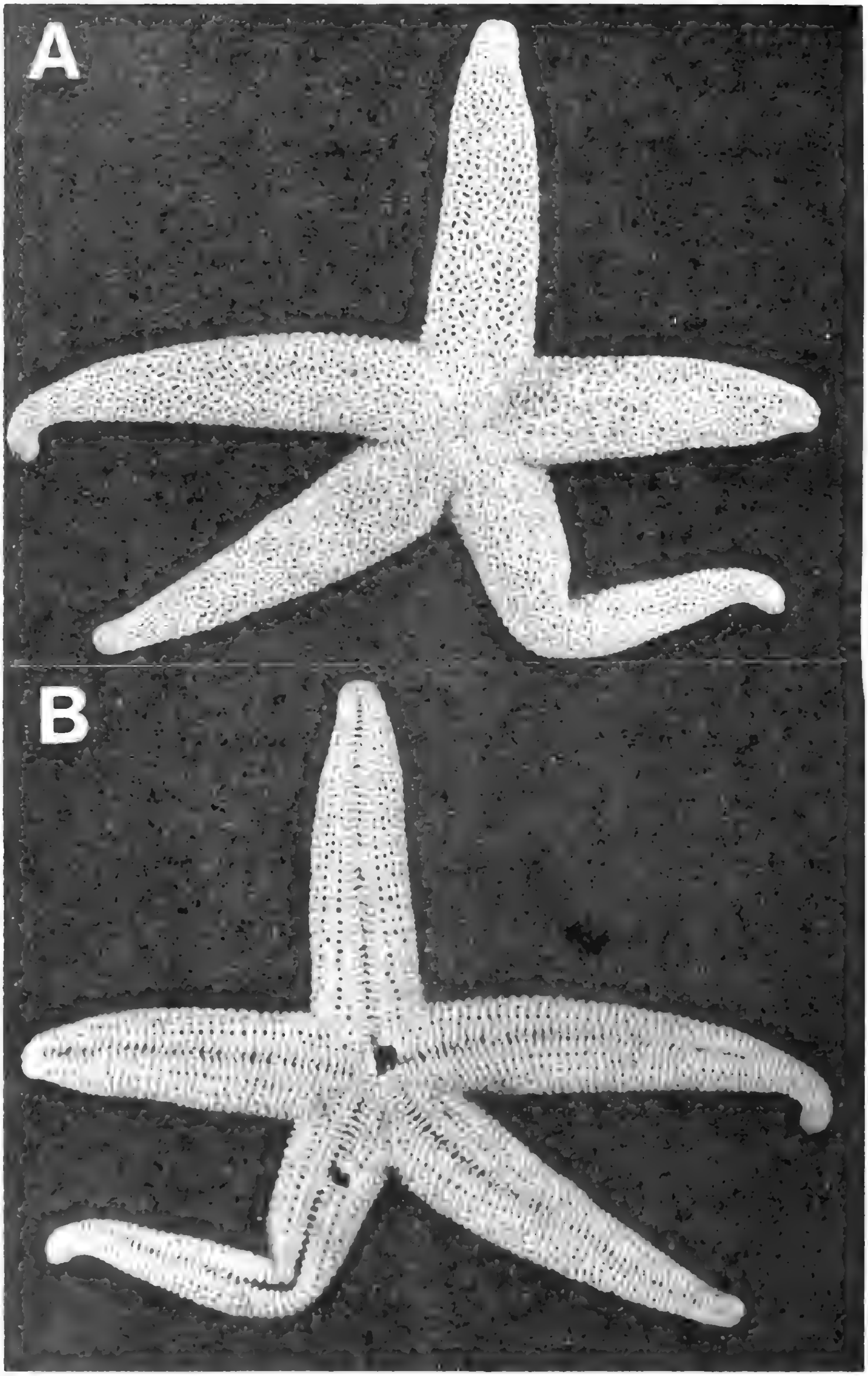

Fig. 2. Odontohenricia endeavouri n. gen. et. sp. (holotype; AM J8792): **A.** abactinal surface; **B.** actinal surface (R = 40mm).

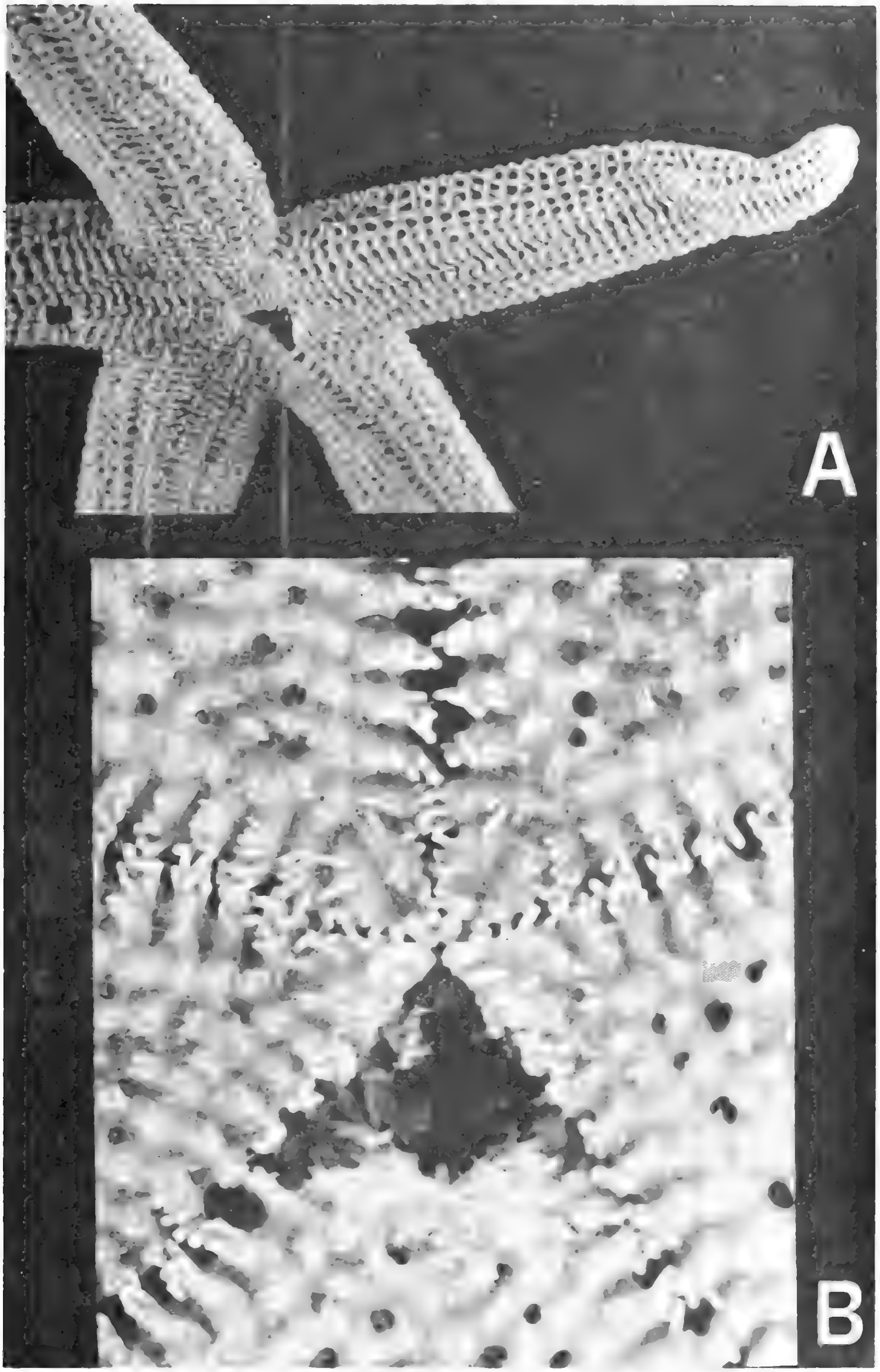

Fig. 3. Odontohenricia endeavouri n. gen. et. sp. (holotype, AM J8792); **A.** lateral view of arm **B.** actinal region showing apical oral spines, adambulacral spines and papulae.

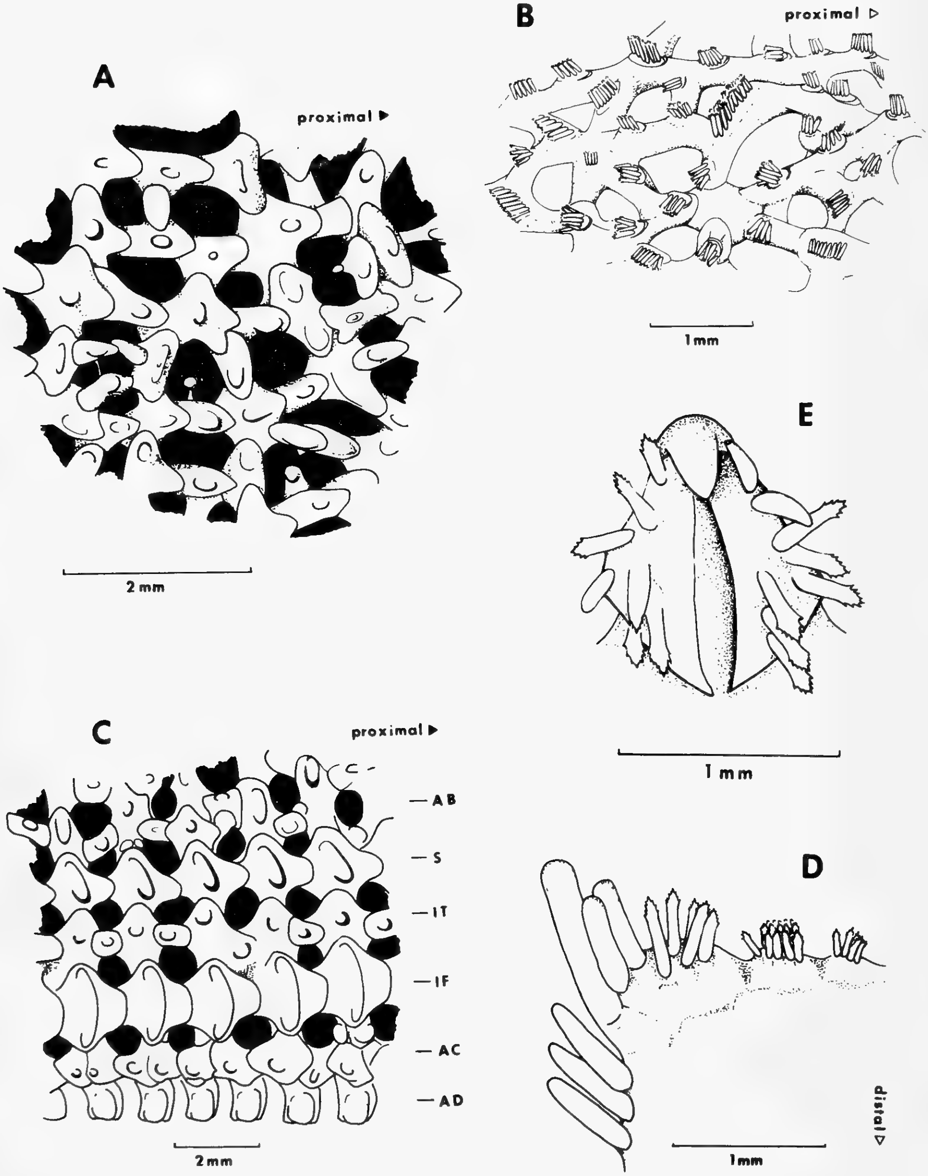

Fig. 4. Odontohenricia endeavouri n. gen. et. sp. (holotype; AM J8792): **A.** denuded abactinal skeleton of arm, (proximal); **B.** abactinal spinelets of arm (proximal); **C.** denuded skeleton of arm, lateral view from ⅓R, distally; AB = abactinal plates, S = superomarginal plates, IT = intermarginal plates, IF = inferomarginal plates, AC = actinal plates, AD = adambulacral plates; **D.** profile view of 2nd adambulacral plate showing alignment of furrow spines and subambulacral spines and with adjacent actinal plates; **E.** actinal view of pair of oral plates showing large, apical, recurved oral spine and suboral spines.

The marginal plates (Figs 3**A**, 4**C**) are distinct due to their size, regular shape and alignment. The superomarginals are quadrilobed, about as long as wide, with a median spinelet bearing ridge oriented obliquely. The inferomarginals are also ridged and quadrilobed, markedly higher than wide, making this series conspicuous.

The intermarginal plates are more or less quadrilobed, bridged with smaller plates. Both the quadrilobed and bridging plates are ridged centrally and bear spinelets. The principal intermarginal series extends ¾R, while a second series consists of a few plates only.

Actinal plates occur in two rows, the first extending almost the ray length, the second only ¼R. The plates are centrally ridged and bear spinelets. There is one papula present between adjacent plates to the marginal series.

A vertical row of 2-3 tapered blunt furrow spines is present within the furrow. The adambulacral plates (Figs 3**B**, 4**D**) bear 2 transverse rows of up to 5 cylindrical subambulacral spines on their actinal surface. The spines decrease in size across the plate. Spines at furrow edge are cylindrical, rounded apically, while those behind are tapered, serrated becoming similar to spinelets on adjacent actinal plates.

Each pair of oral plates is dominated by a large recurved hyaline spine at their common apex, 4(5) dentate spinelets occur on the furrow margin of each plate with 3-4 suboral spines on the actinal surface of each oral plate.

Paratypes: Some variation was found within the 11 designated paratypes. All were 5 rayed R=30-69mm, r=5-12mm except one (AM J3072) which is 6 rayed. The number of intermarginal and actinal series varied from 1-3, extending from ¼-¾R, in the first series, a few plates to ¼R in the second, and a few plates sometimes present as a third. Similarly, the first actinal series may extend between ¾R to R, the second from a few plates to ¼R, and sometimes a few plates formed a third series.

Other material: Some 15 further specimens have been identified. These fall within the variation we recognize within the type series.

Remarks: *O. endeavouri* differs from other known *Odontohenricia* by the arrangement of the abactinal spinelets, the presence of stellate plates in the abactinal skeleton and the elongated inferomarginal plates.

Odontohenricia clarkae n. sp.
Figs 5**A-B**, 6**A-E**

Diagnosis: Rays 5, R=26-33mm, r=4.4-6.6mm, R/r=5-6; rays cylindrical, tapering to a rounded tip; abactinal skeleton reticulate, 2-9 papulae per papular area; plates ridged medially, carrying 6-15 serrated spinelets; marginal plates distinct, with obvious vertical and horizontal alignment of series; plates quadrilobed, with trilobed ridges; inferomarginal plates higher than broad, more elongate than superomarginals, 1-2 intermarginal series; 2-4 actinal series; 1-5 papulae present throughout marginal series, adambulacral plates with 1-2 furrow spines in vertical series, one prominent subambulacral spine on adradial edge of plate with 10-13 subambulacral spines behind in 2 rows; oral plate pair with large apical recurved spine, each plate with 2-3 small spinelets along furrow margin, and an additional 3 suboral spines.

Material examined: Two specimens, holotype and paratype, BM (NH) 1951.5.8.2, 34°33′S 18°20′E, off the Cape of Good Hope, South Africa, 290m.

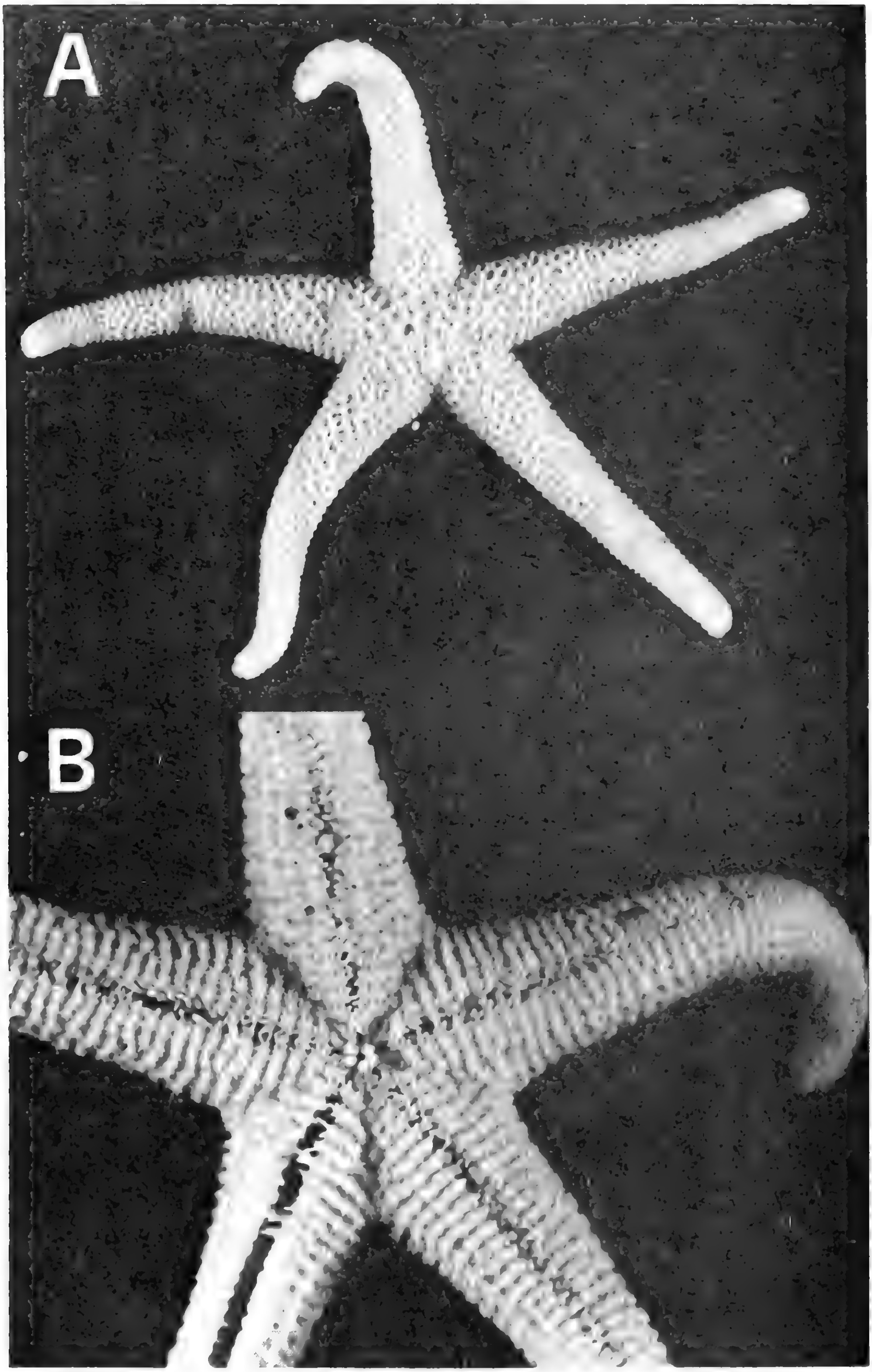

Fig. 5. *Odontohenricia clarkae* n. gen. et. sp. (paratype; BM (NH) 1951. 5.8.2): **A.** abactinal view; **B.** actinal surface, showing apical oral spines, abactinal and marginal spinelets (R = 26mm).

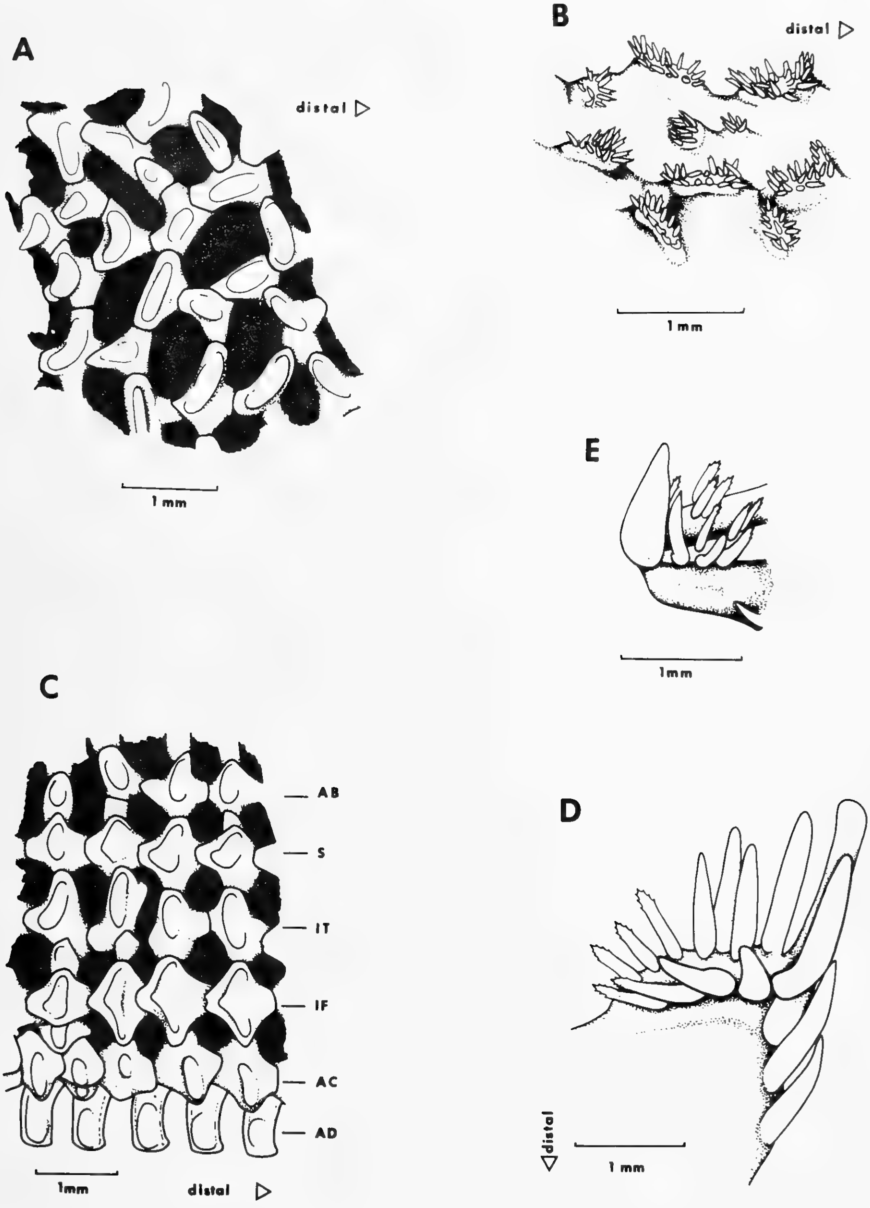

Fig. 6. Odontohenricia clarkae n. gen. et. sp. (holotype; BM (NH) 1951. 5.8.2): **A.** denuded abactinal skeleton of arm (proximal); **B.** abactinal spinelets of arm (proximal); **C.** denuded skeleton of arm, lateral view (proximal); AB = abactinal plates, S = superomarginal plates, IT = intermarginal plates, IF = inferomarginal plates, AC = actinal plates, AD = adambulacral plates; **D.** profile view of 5th adambulacral plate with furrow and subambulacral spines; **E.** oblique-lateral view of pair of oral plates showing large apical oral spine and suboral spines (R = 33mm).

Distribution: At present known only from the type locality.

Etymology: Named for Ailsa Clark for her significant contribution to the knowledge of the echinoderm faunas, including that of southern Africa.

Description: The species has 5 rays, cylindrical and tapering to a rounded tip. Holotype R=33mm, r=6.6mm, R/r=5; paratype R=26mm, r=4.4mm, R/r=5.9. The disc is small. The madreporite occurs interradially at approximately ⅓r.

The abactinal skeleton (Fig. 6**A**) is delicate and reticulate, with 2-9 papulae per papular area, but more commonly 5. The plates are irregular, ranging from bar to crescent shaped, the latter contributing to a scalloped appearance of the abactinal surface (Fig. 5**A**). Each plate is raised centrally into a low ridge, bearing 6-15 spaced, fine, serrate spinelets (0.26mm long, 0.04mm wide) (Fig. 6**B**).

The marginal plates (Fig. 6**C**) are distinct. The plates and their medial ridges are regular in shape and alignment forming a well developed horizontal series. The superomarginals are quadrilobed, higher than broad and each bears a central crescentic to trilobed ridge which carries 6-16 spinelets. The inferomarginals are quadrilobed, being markedly higher than broad. Spine-bearing medial ridges occur similarly to those on the superomarginals. The intermarginal plates are irregularly lobed, bearing vertical or crescentic, spine-bearing, medial ridges, the series extending $^3/_5$R in the holotype, and in the paratype $^2/_5$-½R. The holotype has 2 series of intermarginal plates, the second extending to ¼R. The actinal plates are irregular and quadrilobed, with spined median ridges. The first actinal series extends for $^3/_5$R and a second series, of a few plates in the holotype, and extending ⅓R in the paratype, lies above. The paratype also bears a series of a few plates between the second actinal series and the inferomarginal plates. Papulae are found throughout the marginal series (2-5 per papular area). Between the plates of the actinal series a single papula may be present. The spinelets on all marginal plates are similar to those of the abactinal plates, being irregularly toothed apically. The spinelets (12-18) are spaced on the ridge surface available (Fig. 6**B**).

Within the furrow there is a vertical series of 1-2 smooth tapered furrow spines in the holotype but only a single spine occurs in the paratype. The adambulacral plates (Fig. 6**D**) bear one long smooth subambulacral spine at the furrow edge. Behind these stand 10-13 subambulacral spines, decreasing in height with distance from furrow. The smallest spinelets are similar to those on the abactinal and marginal plates.

Each pair of oral plates (Figs 5**B**, 6**E**) is dominated by a large smooth recurved spine apically. In the paratype each plate also carries 3 spines along the furrow margin and 3 suboral spines on the actinal surface. Some of these spines have been lost in the paratype and completely lost from the holotype through mechanical damage. A small smooth spine is present distally on the lateral face of the oral plate.

Remarks: The variation seen between the holotype and paratype can be attributed to size differences. The crescentic plates abactinally give a scalloped effect not seen in other species of *Odontohenricia* here described. This, with the combined features of the trilobed ridges of the superomarginal and inferomarginal plates, the marked vertical alignment of the marginal series and oral plate armature distinguish this species.

The two specimens described herein were among 3 identified as *Henricia 'abyssalis'* (Perrier), a species known to occur in South African waters (A. M. Clark and Courtman-Stock, 1976).

Odontohenricia fisheri n.sp.

Figs 7**A-B**, 8**A-E**

Henricia leviuscula annectens; Fisher 1911, 291 (part) (non *H. leviuscula annectens* Fisher 1910).

Diagnosis: Rays 5, R=82mm, r=15mm, R/r=5.5, inflated proximally, tapering distally to narrow tip; abactinal skeleton open reticulate, plates ridged medially, 1-5 accessory plates sometimes present in papular areas, 1-7 papulae per area; abactinal spinelets 0.4mm long, 0.08mm wide, tapering to serrated tip, spinelets densely clustered; marginal plates distinct, quadrilobed, ridged medially, spinelets similar to those on abactinal plates; inferomarginals slighty higher than superomarginals; 4 rows of intermarginal plates, principal row extending for ½R; 3 rows of actinal plates extending $^4/_5$R, $^1/_5$R and $^1/_{10}$R respectively; papulae extend to actinal series, with 1 per area; 2 furrow spines in vertical series; adambulacral plate with 3-5 smooth, cylindrical, sometimes spatulate subambulacral spines occurring on the adradial edge, behind which occur 9-11 cylindrical spines, apically serrate or smooth, in 2-3 more or less distinct rows, these subambulacral spines decrease in size across the plate; a large recurved spine occurs at the apex of the jaw, with 12-15 smaller, smooth suboral spines occurring on the adradial and actinal surfaces of the oral plates.

Material examined: One specimen, holotype, U.S. National Museum E3838, 48°33′N, 124°53′W, off Washington, U.S.A., 108m.

Distribution: At present known only from the type location.

Etymology: Named for Dr W. K. Fisher who has contributed much to our knowledge of the classification of sea-stars.

Description: Rays 5, long and cylindrical, inflated proximally and tapering to rounded tip (Fig. 7). R=82mm, r=15mm, R/r=5.5. The disc is relatively small. The madreporite, is ridged and spine-bearing, occurring interradially, at about ½r.

The abactinal plates are irregularly bar to crescent shaped and form an irregular reticulum. Frequently (at least proximally) additional small plates are present within the papular areas (Fig. 8**A**). These areas may contain 1-7 papulae, but more commonly 3-4. The skeletal plates are raised medially forming low ridges. These ridges bear dense clusters of 3-24, but more commonly 15-20 tapered spinelets (length: 0.4mm, width 0.08mm) which are serrated apically (Fig. 8**B**).

The marginal series are distinct, the plates being aligned vertically and horizontally (Fig. 8**C**). The superomarginal plates are quadrilobed, higher than broad, each with an oblique crescentic ridge bearing a dense cluster of spinelets (24-28). The inferomarginal plates are quadrilobed, as high as wide, but larger than the superomarginals. Medial ridges of these plates are crescentic to ovoid in shape and carry dense clusters of spinelets (23-34).

The intermarginal plates are somewhat rectangular but may be enlarged basally or lobed laterally, and bear circular to ovoid medial ridges bearing spinelets. One intermarginal series extends approximately ½R although not clearly defined throughout. A second series between the first intermarginal and the inferomarginal series extends $^1/_6$R. In addition, a few plates occur between the superomarginal series and the principal intermarginal series, and also between the second intermarginal and inferomarginal series. The actinal plates are quadrilobed, as high as wide, each with an ovoid, medial, spinelet-bearing ridge (13-26 spinelets). The first series extends $^4/_5$R, a second

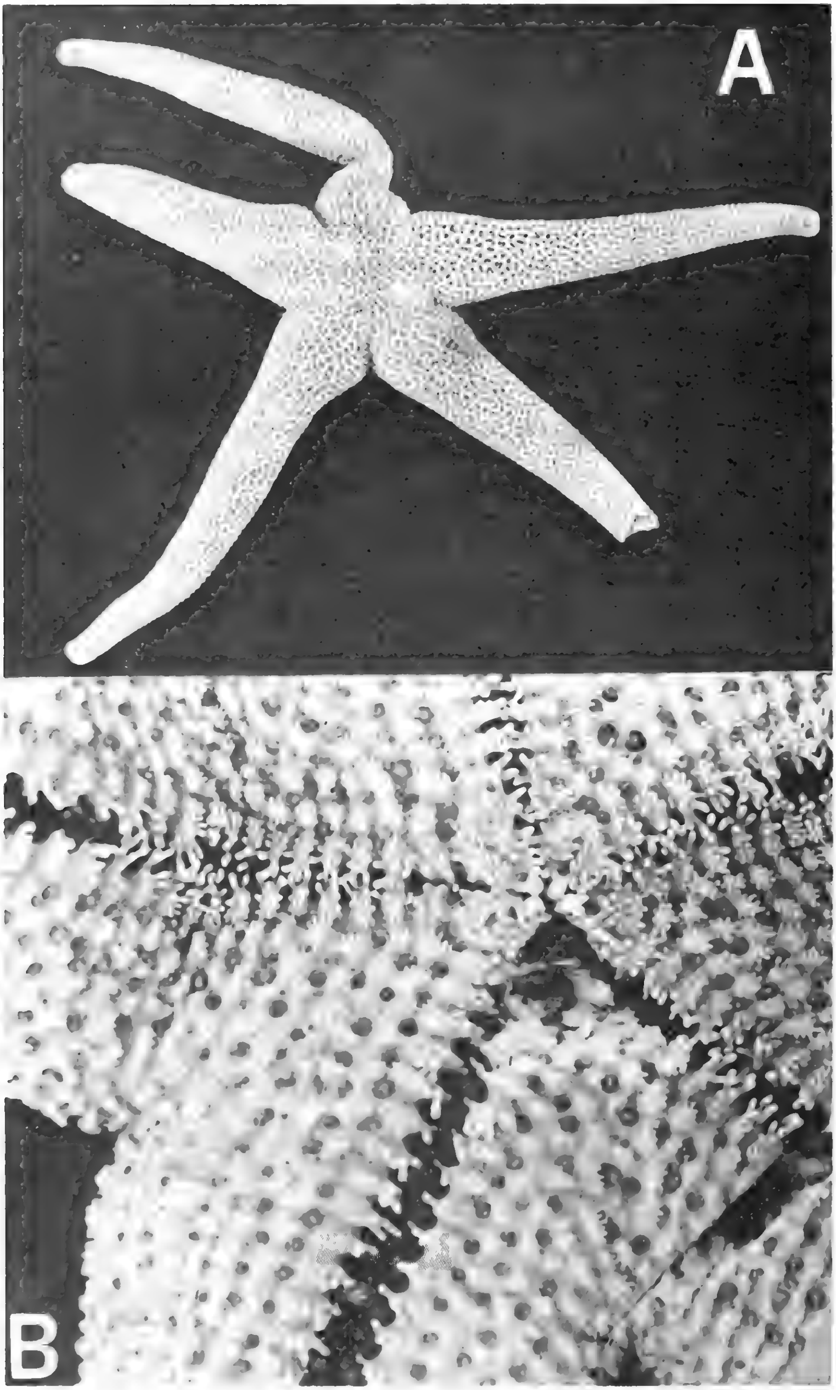

Fig. 7. Odontohenricia fisheri n. gen. et. sp. (holotype; U.S. National Museum E3838): **A.** abactinal surface; **B.**actinal surface, showing apical oral spines, actinal papulae and adambulacral and actinal spinature (R = 82mm).

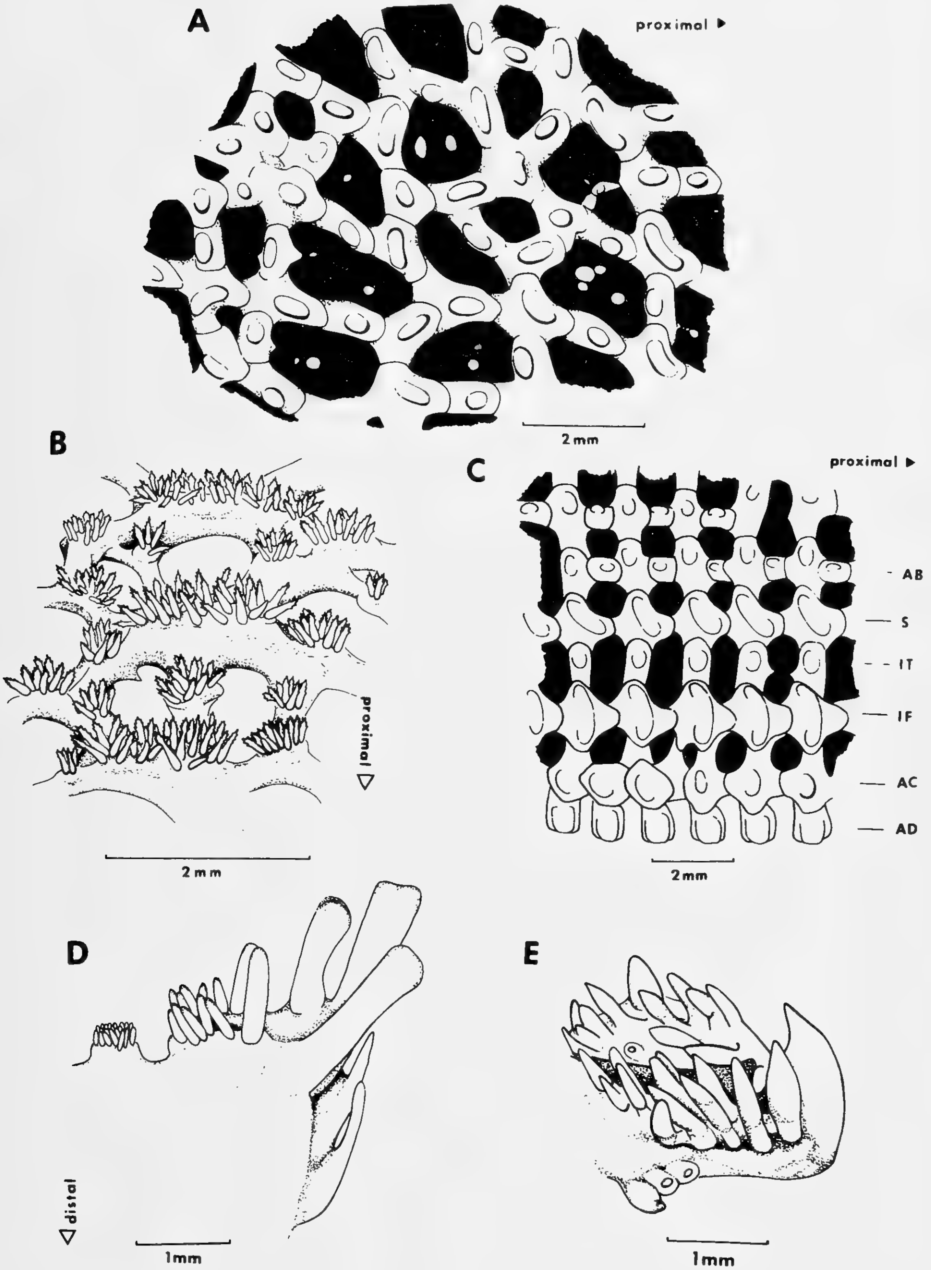

Fig. 8. Odontohenricia fisheri n. gen. et. sp. (holotype; U.S. National Museum E3838): **A.** denuded abactinal skeleton of arm (proximal); **B.** abactinal spinelets of arm (proximal); **C.** denuded skeleton of arm, lateral view from 11th to 16th superomarginal plate; AB = abactinal plates, S = superomarginal plates, IT = intermarginal plates, IF = inferomarginal plates, AC = actinal plates, AD = adambulacral plate; **D.** profile view of 9th adambulacral plate showing furrow and subambulacral spines and with adjacent actinal plate and spinelets; **E.** oblique-lateral view of oral plate pair with large apical and suboral spines.

series to $^{1}/_{5}$R, and a third to $^{1}/_{10}$R. The spinelets occurring on the marginal plates are similar to those found abactinally. Papulae extend throughout the marginal series with one papula between actinal and inferomarginal plates and elsewhere 1-5 per papular area.

There are 2 spines in vertical series within the furrow. The adambulacral plates bear 3-5 smooth, elongate and sometimes spatulate spines. Behind these are 9-11 cylindrical spines which may be serrated apically or smooth. These form 2-3 more or less distinct rows, although they may also be clustered (Fig. 8**D**).

Each pair of oral plates bears a large, smooth, recurved, hyaline spine apically (Fig. 8**E**). Each oral plate also bears 5-6 small cylindrical spines along the furrow margin, with an irregular row of 4-6 subambulacral spines on the actinal surface of the plate. In addition there are 3-5 subambulacral spines distally.

Remarks: *Odontohenricia fisheri* is clearly distinguishable from other species of *Odontohenricia* by its size, the presence of additional plates within the abactinal reticulum, the rectangular intermarginal plates and the abundance of oral plate spines and other skeletal plate spines. Fisher (1911) identified this specimen as *Henricia leviuscula annectens*.

Odontohenricia hayashii n.sp.

Figs 9**A-B**, 10**A-F**

Diagnosis: Rays 5, R=35mm, r=6mm, R/r=5.9mm; slender, tapering to rounded tip; abactinal skeleton reticulate, 1-5 papulae per area; abactinal spinelets, 0.48mm long, 0.08mm wide, slender and apically dentate, 1-9 spinelets per plate in tufts or irregular rows; marginal plates prominent, superomarginal, inferomarginal and actinal series being similar in shape size and alignment, all with oblique medial ridges bearing spinelets; intermarginal plates irregular, lobed, frequently fused, in 3 series, first row to ¼R and the second and third comprising a few plates only, 2 actinal series to ¾R and $^{1}/_{5}$R respectively, papulae present between marginals and actinals, 1-4 per papular area; plates show widespread extensions which restrict the papular area, marginal spinelets as for abactinal plates; 1(2) furrow spines, adambulacral plates with a single prominent subambulacral spine on adradial edge, and with 8-10 cylindrical subambulacral spines in, more or less, 2 rows, decreasing in size across the adambulacral plate; oral plates with recurved, hyaline, apical spine, additional 7(8) regular suboral spines on each plate.

Material examined: one specimen, holotype, U.S. National Museum E34052, Sagami Bay, Honshu, 35°50′N, 139°35′E, Japan, 152-289m.

Distribution: at present known only from type locality.

Etymology: named for Dr Ryoji Hayashi, who has contributed much to our knowledge of the Japanese sea-stars.

Description: Rays 5, cylindrical and slender, tapering to a rounded tip (Fig. 9). R=35mm, r=6mm, R/r=5.9mm. The disc is relatively small. The madreporite occurs interradially, ½R.

The abactinal plates are tapered, bar and quadrilobed in shape, overlapping to form a fine, open, more or less regular reticulate skeleton (Figs 10**A**, **B**). The plates are raised medially and bear 1-9 but more usually 5-7 spinelets in tufts or irregular rows.

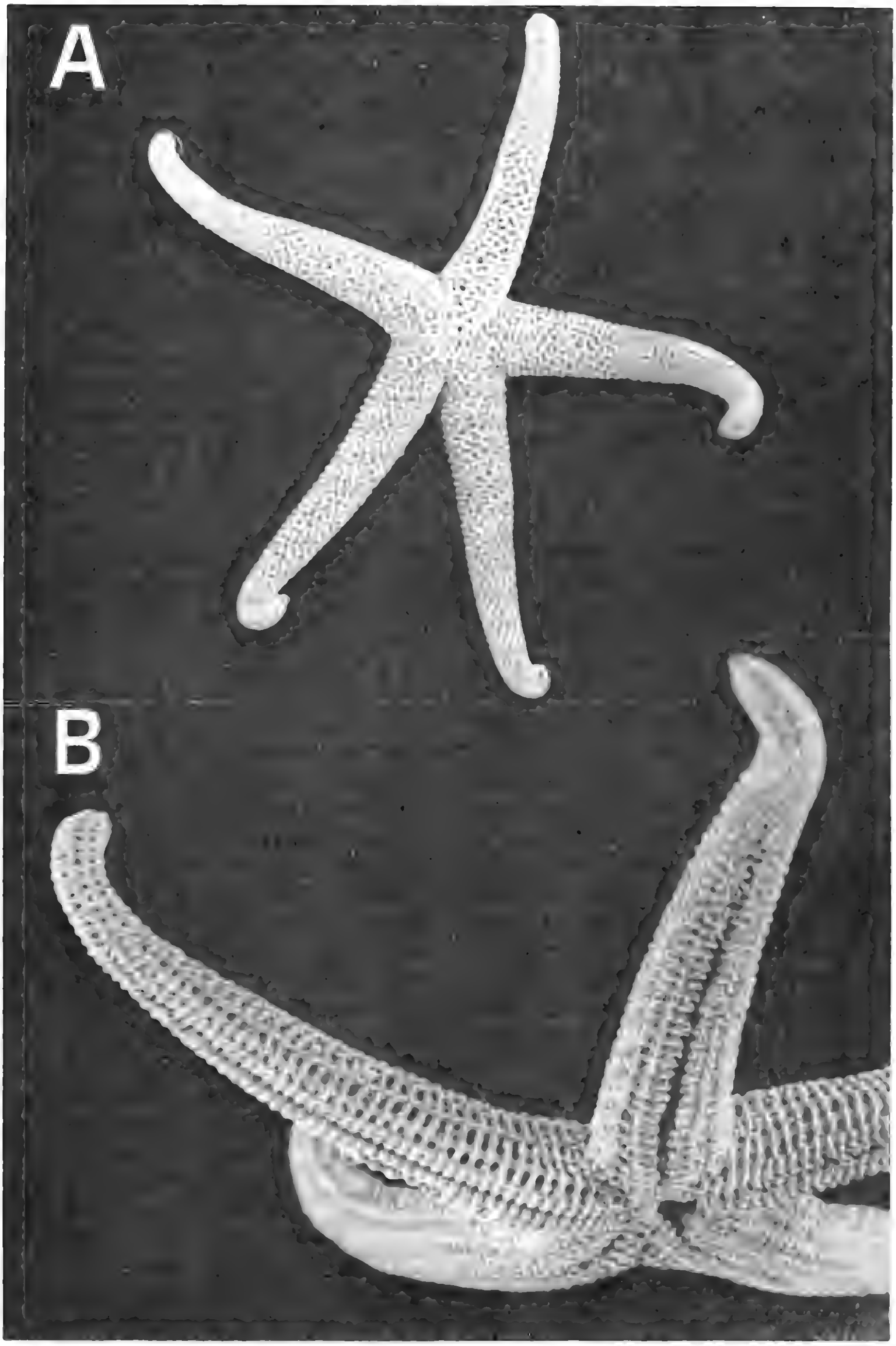

Fig. 9. Odontohenricia hayashii n. gen. et. sp. (holotype; U.S. National Museum 38307): **A.** abactinal surface; **B.** lateral view of arm (R = 35mm).

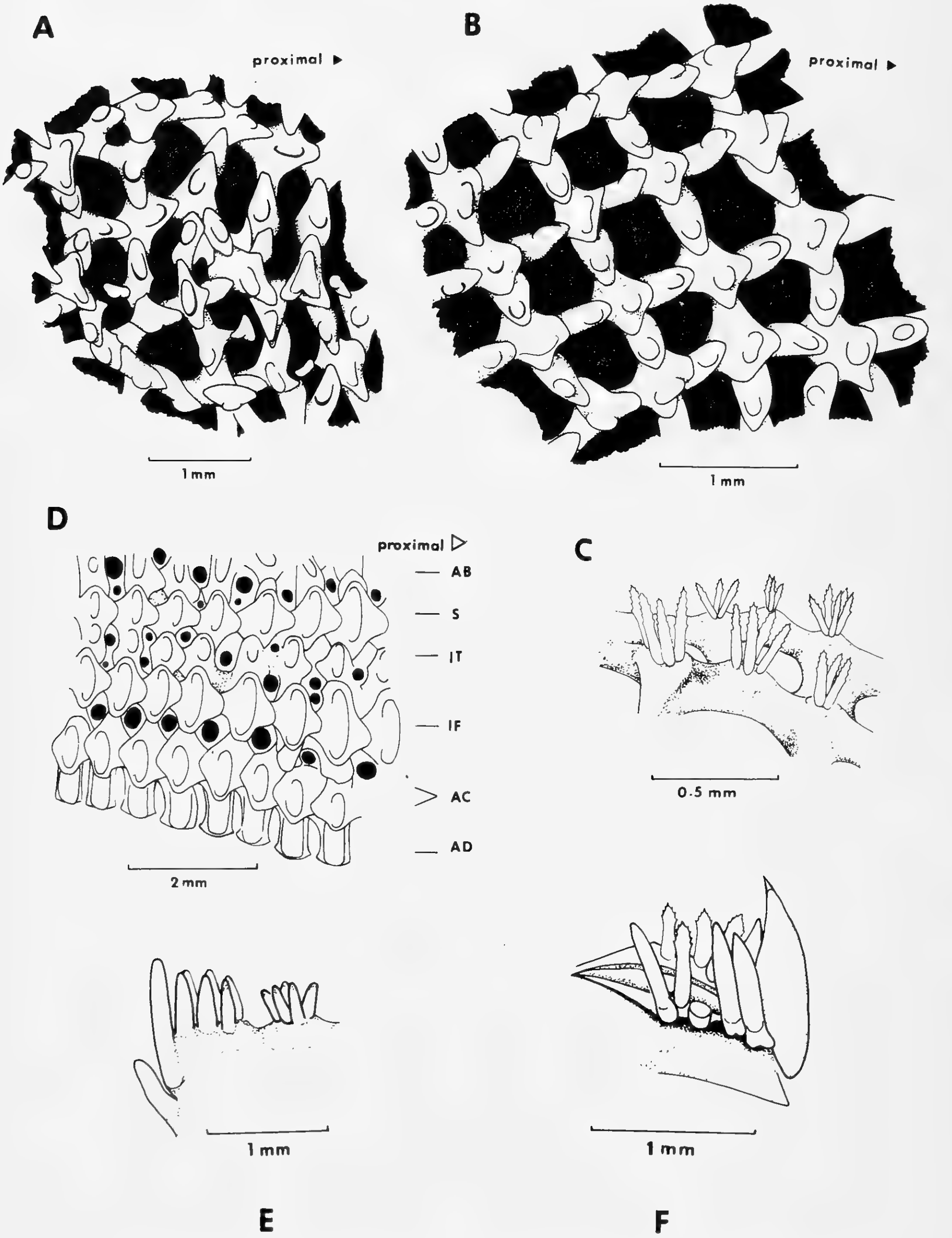

Fig. 10. Odontohenricia hayashii n. gen. et. sp. (holotype; U.S. National Museum 38307): **A.** denuded abactinal skeleton of arm (proximal); **B.** denuded abactinal skeleton of arm (distal); **C.** abactinal spinelets of arm (proximal); **D.** denuded skeleton of arm, lateral view from 7th to 13th superomarginal plate; AB = abactinal plates, S = superomarginal plates, IT = intermarginal plates, IF = inferomarginal plates, AC = actinal plates, AD = adambulacral plate; **E.** profile view of adambulacral plate showing furrow and subambulacral spines and with adjacent actinal plate (composite drawing from 13th and 14th plates due to damage); **F.** oblique-lateral view of oral plate pair with large apical spine and suboral spines.

The spinelets are 0.48mm long, 0.08mm wide and dentate apically. The papular areas are small, bearing 1-5 but more commonly 2-3 papulae per area.

The superomarginal, inferomarginal and actinal plates are distinct, being of comparable shape and size, and regularly aligned (Fig. 10**D**). They are quadrilobed, as high as wide, and bear a transverse, medial, spinelet bearing ridge. The intermarginal plates are irregularly lobed and frequently fused. There is one principal series, extending ½R, and 2 additional series of only a few plates, one above and one below the principal series. These plates are also spined and ridged medially, and are aligned with those of the other marginal series. There are 2 actinal series of plates, the first extending ¾R and a second extending $^{1}/_{5}$R. Papulae are present between these marginal series, usually 1 per papula area, rarely 2. There is extensive broadening of plates throughout the marginal series, excluding spaces for papulae. The spinelets found on the marginal plate ridges are as those of abactinal plates. Within the furrow there is one, sometimes 2 cylindrical spines in vertical series. There is a single prominent, cylindrical subambulacral spine on the adradial edge of the adambulacral plate, behind which are 8-10 cylindrical, round-tipped subambulacral spines in 2 more or less regular rows (Fig. 10**E**). These spines decrease in height and breadth with distance from the furrow. The oral plate pair is dominated by a large smooth recurved apical spine. Four regular spines are also found along the furrow margin of the oral plate, with 1-2 additional suboral spines (Fig. 10**F**).

Remarks: This species is clearly distinguished from other *Odontohenricia* here described by the small clusters of long abactinal spinelets, and the extension to the marginal plates. A. H. Clark identified 2 specimens from 'Albatross' station 3749 as *Henricia densispina* (Sladen) one of which we describe here as the holotype of *O. hayashii*. The identity of the second specimen may also be questionable though *H. densispina* has been recorded from Japanese waters by Hayashi (1940).

ACKNOWLEDGEMENTS

We wish to thank the following colleagues for the loan of specimens. Miss A. M. Clark, British Museum (Natural History), London, U.K.; Dr D. L. Pawson and Miss M. Downey, United States National Museum (Smithsonian Institution), Washington, D.C., U.S.A.; Ms Sue Boyd, Museum of Victoria, Melbourne, Vic., Australia. We also thank Mr Ken Graham for collecting material on FRV 'Kapala' and New South Wales State Fisheries for donating the specimens to the Australian Museum. The senior author wishes to acknowledge support from the Marine Sciences and Technologies Grant Scheme (MST: 84/2092).

References

CLARK, A. M., and COURTMAN-STOCK, J., 1976. — *The Echinoderms of Southern Africa.* London: British Museum (Natural History). 1-277, 276 figs.

CLARK, H. L., 1916. — Report on the sea-lilies, star fishes, brittle-stars and sea-urchins obtained by the F.I.S. 'Endeavour' on the coasts of Queensland, N.S.W., Tasmania, Victoria, S. Australia and W. Australia. *Endeavour Res.* 4:1-123, 11 figs, 44 pls.

——, 1946. — The echinoderm fauna of Australia. *Publs. Carnegie Instn* No. 566: 1-567.

FISHER, W. K., 1910. — New starfishes from the North Pacific. II. Spinulosa. *Zool. Anz.* 35: 568-574.

——, 1911. — Asteroidea of the North Pacific and adjacent waters Part 1. Phanerozonia and Spinulosa. *Bull. U.S. natn. Mus.* 76: 419pp, 122 pls.

——, 1940. — Asteroidea. *Discovery Rep.*, 20: 69-306, 23 pls.

GRAY, J. E., 1840. — A synopsis of the genera and species of the Class Hypostoma (*Asterias* Linn.). *Ann. Mag. nat. Hist.* (1) 6: 175-184.

HAYASHI, R., 1940. — Contributions to the classification of the sea-stars of Japan. I. Spinulosa. *J. Fac. Sci. Hokkaido Imp. Univ.* (6) 7(3): 107-204, pls vii-xiii.

PERRIER, E., 1891. — Echinodermes. I. Stellerides. *Rept. Mission sci. du Cap Horn* 1882-83. 6 (3) Zoologie: K1-K198, pls. 1-13.

SLADEN, W. P., 1889. — Asteroidea. *Rep. scient. Results Voy. 'Challenger'* (Zool.). 30: 893pp, 117 pls.

ROWE, F. W. E., and ALBERTSON, E. L., 1987a. — The echinoderm genus *Henricia* Gray, 1840 (Asteroidea: Echinasteridae) in southern and southeastern Australian waters, with the description of a new species. *Proc. Linn. Soc. N.S.W.* 109: 183-194.

——, and ——, 1987b. — A new species in the echinasterid genus *Echinaster* Müller and Troschel, 1840 (Echinodermata: Asteroidea) from southeastern Australia and Norfolk Island. *Proc. Linn. Soc. N.S.W.* 109: 195-202.

ERRATUM

HELENE A. MARTIN
Presidential Address. Cainozoic History of the Vegetation and Climate of the Lachlan River Region, New South Wales. *Proc. Linn. Soc. N.S.W.* 109 (4), (1986) 1987: 213-257.

p.244, lines 45-46, should be:

Today, the mean annual precipitation for Hillston is about 350mm, Forbes 520mm to 535mm and Cowra 610mm to 630mm.

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VOLUME 110
NUMBER 2

THE SIR WILLIAM MACLEAY MEMORIAL LECTURE 1987

The elastic-sided Gumleaf, or: The Rubber Cuticle and other Studies of the *Corymbosae*

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Australian National University, Canberra

[Delivered by D. J. CARR 30 September 1987]

Introduction: the rubber cuticle of the *Corymbosae*

In 1908, the Sydney phytochemist Henry G. Smith, of the Technological Museum, published an account of his analysis of the cuticles of *Eucalyptus gummifera* and those of two species of *Angophora*. He showed that, using suitable solvents, a material could be extracted from young leaves of these species which had chemical and physical properties identical with those of natural rubber (caoutchouc). It was soluble in chloroform, and in absolute ether but not in petroleum ether. Various tests, including melting point and ability to be vulcanized, convinced Smith that the material was indeed rubber. It has long been known that the cuticles of young leaves of species like *E. gummifera*, spotted gum (*E. maculata*), and red flowering gum (*E. ficifolia*), are easily removed almost intact from the leaf surfaces and have the elastic properties of rubber. Later on, as the leaves mature and become fully developed, the cuticle undergoes changes which prevent it from being stripped off the leaves. This extraordinary discovery has not rated mention in any of the botanical textbooks, in the many reviews of recent decades on the topic of the plant cuticle or in two monographs devoted to that subject (Martin and Juniper, 1970; Cutler *et al.*, 1982). The only reference we have been able to find is in the 2nd Edition of Metcalfe and Chalk (an expensive, poor relation of the magnificent first edition), in which Metcalfe (1983) reported that 'the secretion of a rubbery substance from epidermal papillae on young shoots of three species of *Angophora* and fourteen species of *Eucalyptus* belonging to the section *Corymbosae* (Myrtaceae) has been reported by Welch (1923)'. Metcalfe thus added confusion to the already confused views of Welch, who in describing the papillate epidermis of the *Corymbosae* as a secretory tissue, ignored the fact that all shoot epidermes which secrete a cuticular layer are also, *ipso facto*, secretory tissues, whether papillate or not. Welch was somewhat misled by the fact that during embedding in paraffin the rubber tends to dissolve in the embedding medium and be at least partially lost. Metcalfe failed to follow up the reference to Smith's work given by Welch. Moreover one of Welch's 14 eucalypts is '*E. santalifolia*', which, as he points out, does *not* belong to the *Corymbosae*. Nor, as Blake (1953) later pointed out, should *E. tessellaris*, another of Welch's species, be included in the *Corymbosae*. Welch did, at least, recognize the material covering the leaves as a *cuticle* and not, to use Metcalfe's phrase, mere 'rubbery secretions'. In his article on 'Secretory Structures: cells, cavities and canals', Metcalfe appears to have followed Nelsonian principles in turning a blind eye to much of the recent literature.

In 1956, when we commenced our studies of the biology of the eucalypts, we repeated Smith's extractions and most of his tests, using young developing leaves of *E. ficifolia* grown in cultivation in Melbourne. We were not only able to verify Smith's

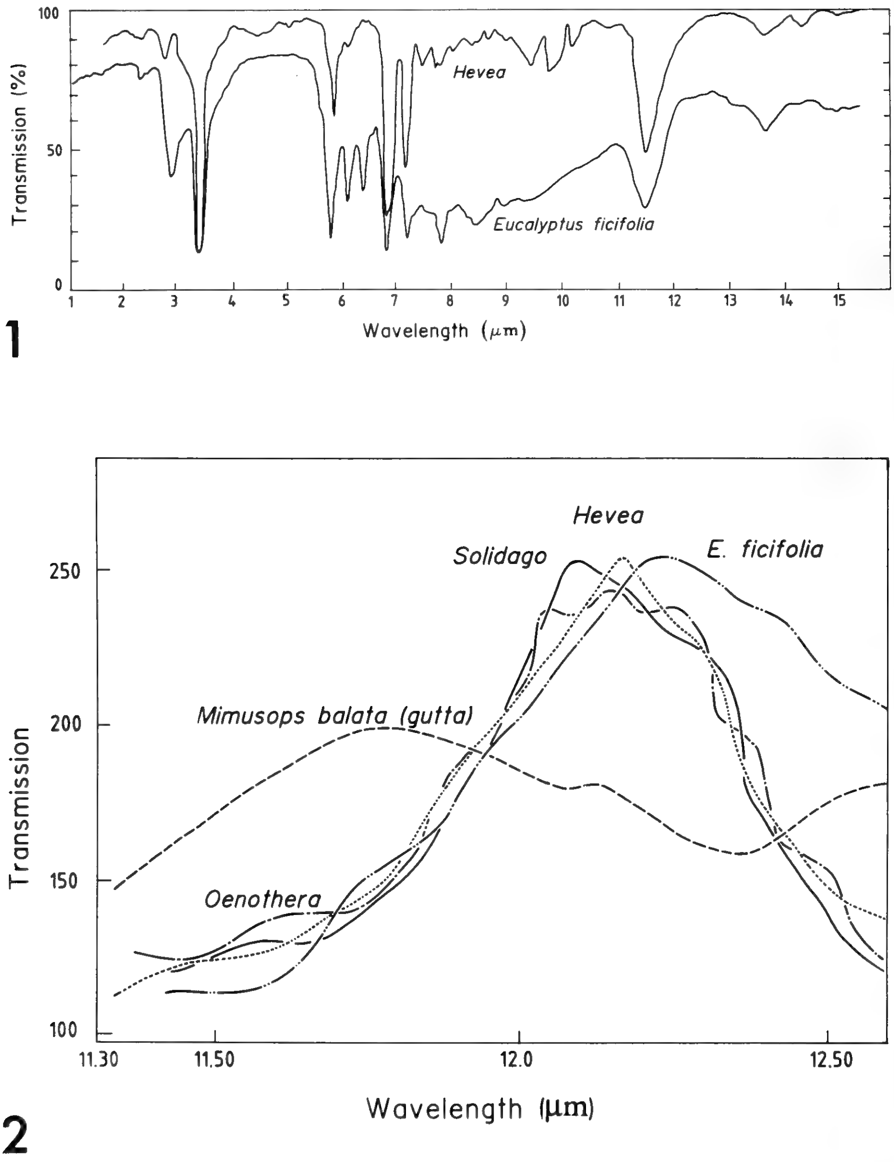


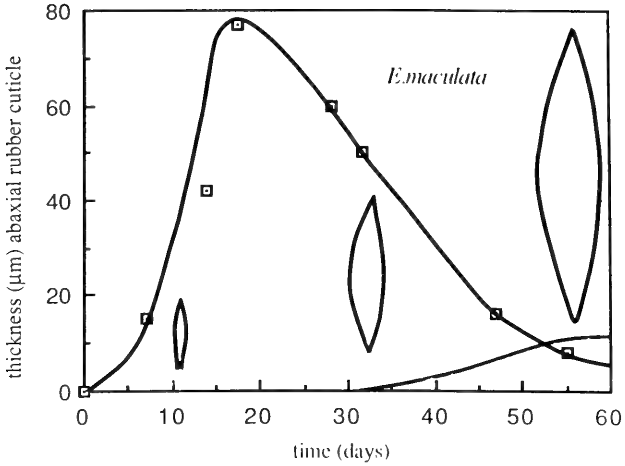
Fig. 1. Infra-red transmission spectrograms; abscissa, microns. **1.** Rubber from *Hevea brasiliensis* and a cuticle preparation from *Eucalyptus ficifolia.* **2.** Comparisons between rubber from various sources, gutta percha, and a cuticle preparation from *Eucalyptus ficifolia.* (Data courtesy Dr T. P. O'Brien and the late Sterling B. Hendricks).

claims, but we also were able to produce little balls of rubber with a very satisfactory bounce. The most favoured method for the identification of rubber is infra-red absorption spectroscopy. Dr T. P. O'Brien, a former student of ours, then employed at ICI in Melbourne, ran some IR absorption spectra of whole cuticles and arranged to send them for comment to Sterling B. Hendricks at the Beltsville Laboratory of the US Department of Agriculture (Fig. 1). Dr Hendricks, by training a physicist and a spectroscopist who had worked with Linus Pauling, had been involved during the last World War in a programme of investigation of various plants (e.g. guayule and the kok-saghyz dandelion) as sources of natural rubber. He examined the IR spectra and in reply to Dr O'Brien stated that 'your samples appear to me on the basis of absorption in the region of 12 microns' (a critical region) 'to be rubber'. More recently we repeated the extraction of rubber from young leaves of *E. calophylla* sent to us by Mrs M. J. Hamersley from Western Australia. Using the samples thus obtained we carried out the chemical test known as Weber's test for rubber. A small sample, 50mg, is cut into fine pieces and put into a test tube. A drop of bromine is added and the test tube is warmed for 30 seconds on a water bath. Then a gram of solid phenol is added. Natural rubber gives a violet coloration, but synthetic rubbers, such as neoprene, give only a weak reaction. Needless to say, the rubber samples from *E. calophylla* gave a strong positive reaction.

The two eucalypt species mentioned so far belong to a group commonly called bloodwoods, or botanically the *Corymbosae.* Following Smith's publication, Maiden (1908-1928) and Welch (1923) claimed to have observed rubber in a variety of species of eucalypts in other taxonomic groups. We have no evidence on this point, although it is inherently not unlikely.

The rubber cuticle is layered

In a number of ways, the cuticle of the *Corymbosae* is different from that of other angiosperms. The consensus of opinion appears to be that, in angiosperms generally, the cuticle steadily increases in thickness as the leaf or stem grows. In the *Corymbosae* the cuticle of the leaf increases in thickness only until the leaf is between a third and a half fully-grown. It then decreases in thickness until near maturity (Fig. 2). The parameters on which these graphs were constructed are discussed in our recent book, *Eucalyptus II.* We would emphasize that much more information (data on plastochrone duration, measurements of the duration and extent of lamina growth, measurements of average cuticle thickness during growth) is needed to establish and quantify these concepts but there can be no doubt that the cuticle thickness does increase and then decrease. This can be seen from a hand-section of a leafy bud of a species such as *E. gummifera.* Clearly then, the rubber cuticle is laid down at an early stage on the surface of the leaf primordium and is subsequently stretched and thins out during what used to be called the 'grand phase of growth' of the leaf. The cuticle remains thick over the midrib and margins of the leaf which expand mainly in length and thickness, especially on the lower surface, (thus increasing its area relative to the upper surface) during the later phases of leaf growth. Welch measured the thickness of the cuticle on a leaf of *E. gummifera* less than 1 millimetre wide to be between 170 and 185μm. Our own measurements of *E. maculata* grown in Canberra show a much more modest maximum thickness. Since the leaves appear in pairs in the buds, with the inner (adaxial) faces of each pair adherent, the thickness of the cuticle on those surfaces lags behind that of the freer abaxial surfaces. Later on, the thickness of the cuticle on the upper surface catches up and at maturity is thicker than that of the lower surface. This is due to the fact that, at a late stage in leaf expansion, the epidermal cells begin to lay down layers of cutinized cuticle (Fig. 3). These develop to a greater thickness on the upper surface than on the lower. They are also thicker on the midrib and margin than elsewhere. Stomata are initiated and begin to break through to the outer surface of the cuticle at or just before the time the leaf is half fully-grown, while the cuticle is beginning to be stretched and thin out. All the stomata are already formed by the time the cuticularized layers begin to be laid down. We shall return to the stomata later on. The flower bud and its constituent parts, such as the sepals, petals, style, stamens and the loculi of the ovary are also covered with



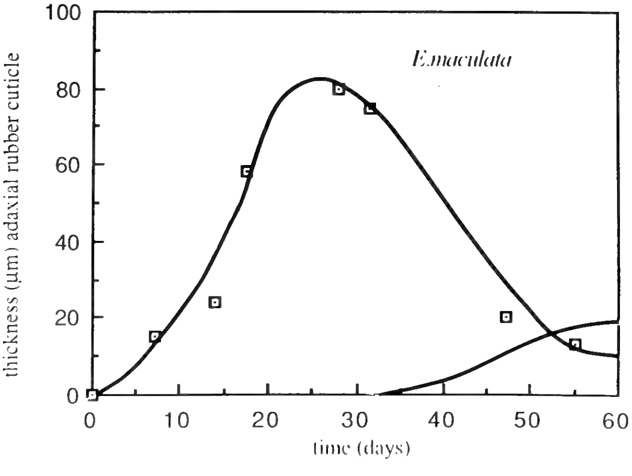


Fig. 2. Graphs to show changes in the thickness of the abaxial (upper graph) and adaxial cuticle of an adult leaf of *E. maculata*. The lines on the lower right of each graph beginning after c.32 days, show the formation of the cuticularized layers underlying the rubber cuticle.

a rubber cuticle, which is often massively thick, and, at maturity, is not underlain by cuticularized layers.

By suitable staining one can demonstrate that the whole of the thick rubber cuticle consists of layers, each consisting of a thin dark layer and a thicker lightly-staining one (Fig. 4). It is often possible to count the layers in a section of the leaf and in a leaf of *E. maculata* estimated to be between 30 and 40 days old, when the cuticle of the adaxial surface is at its maximum thickness, the number of layers is between 30 and 40. This is

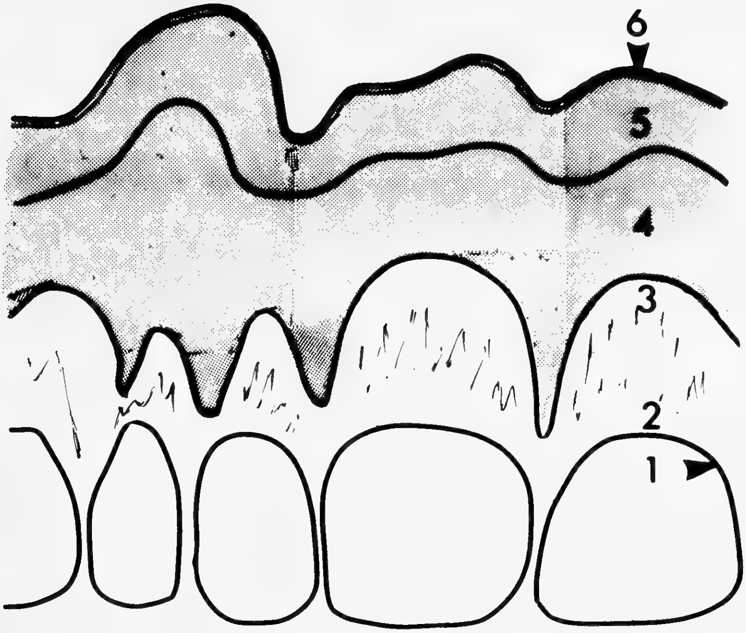


Fig. 3. Diagram to show zonation in the cuticle of a mature, fully-grown leaf of a species of *Corymbosae*. 1, cell wall. 2, 3 cuticularized layer, layer 3 with radial striae. 4, 5 zones of rubber cuticle, the layers well-spaced in 4, closely-spaced in 5. 6, the 'cuticle proper'.

at least presumptive evidence that each bilayer is the product of a single day's secretory activity on the part of the epidermis. A similar diurnal layering is well-known for the cell-walls of certain algae and for the hairs on the seeds of cotton. Moreover, the cuticles of insects have diurnally-produced layers (Neville, 1963). The difference in density between the two portions of a bilayer may reflect different packing densities of the rubber in them or perhaps differences in ancillary materials associated with the layers. Again, we wish to stress that much more work is needed to establish the diurnal rhythm in rubber production, the nature of the differences in the bilayers, the nature of ancillary materials in the rubber cuticle etc.

Stomatal breakthrough in the *Corymbosae*

As we have already shown in studies of the stomatal development in other groups of eucalypts, the stomatal initials appear and the full structure of the guard cells develops, including the split between them, while the guard cells are completely covered by an unbroken cuticle (Fig. 5). Above the line of closure of the guard cells a split must develop in the cuticle to give access to the atmosphere. We have provided evidence from light microscopy which supports the view that this split, resulting in *stomatal breakthrough*, develops by a process of digestion of the cuticle above the guard cells, probably by enzymes secreted by them into the cuticle (Carr and Carr, 1978; Carr and Carr, in preparation). The hole in the outer surface of the cuticle which leads to the guard cells we termed the *ostiole* (Carr and Carr, 1978). Although an essential part of the functional stoma, and, in thick cuticles, often smaller in area than the pore between the guard cells of the open stoma, it had not previously been given a name. Stace (1965) ignores it; Wilkinson (1979) calls it 'the outer stomatal ledge aperture', a long-winded appellation

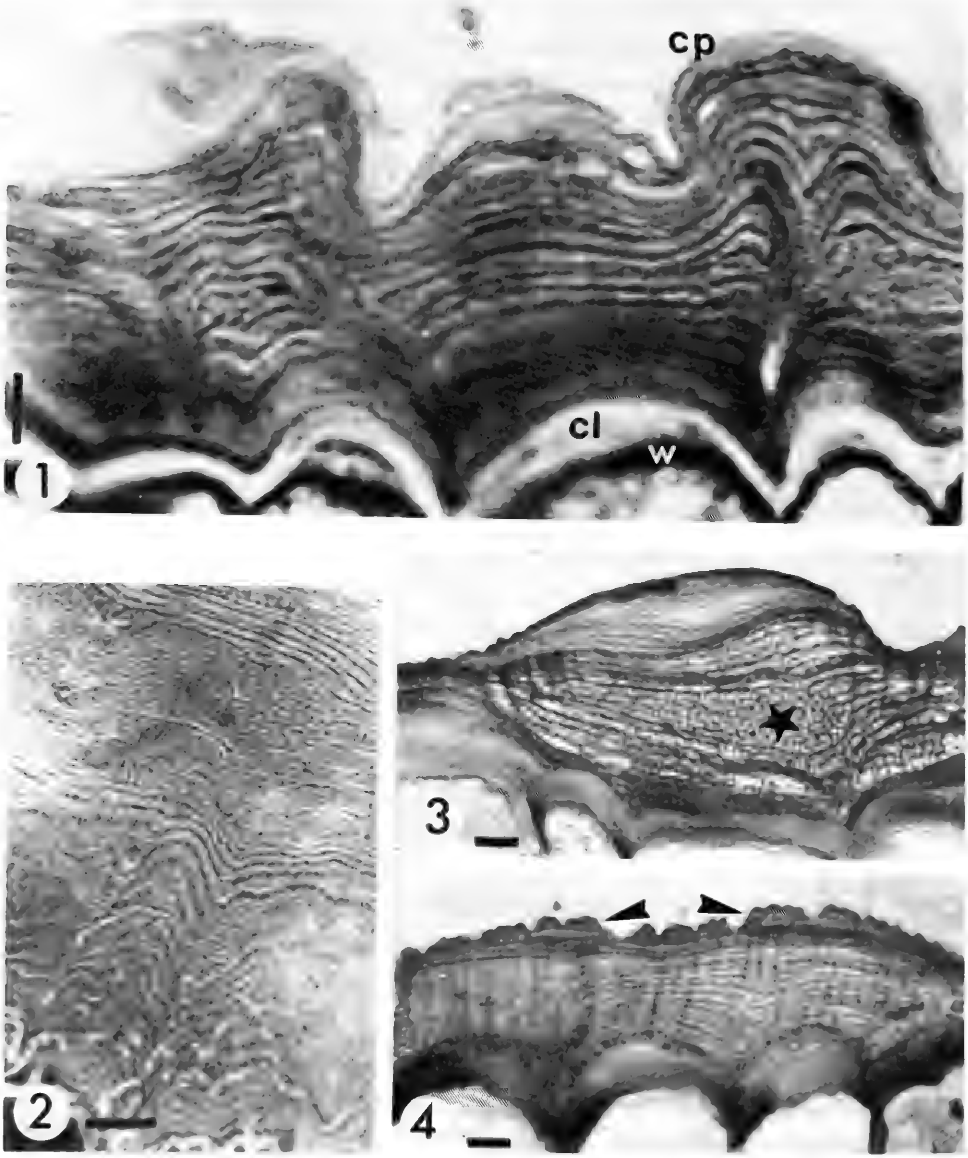


Fig. 4. Lamellate rubber cuticle of developing leaves of *E. maculata*. **1**, **3**, **4** adaxial surface, **2** abaxial surface. **2** leaf about half fully expanded; **3**, **4** fully expanded. In **2**, the number of bilayers (a light zone plus a dark line) is between 30 and 40. In **3** the asterisk indicates a widening of one of the light zones. In **4** arrows indicate positions where losses of outer layers can be observed. cp, cuticle proper; cl, cuticularized layer just beginning to be formed; w, cell wall. Scale bars, 10μm.

which is wrong for sunken stomata (e.g. those of *Proteaceae* spp., *Aloe* spp., *Ficus* spp., *Eucalyptus incrassata* (Carr and Carr, 1978), species of the *Bisectae* (*Eucalyptus*) and of the *Lehmannianae* (*Eucalyptus*) (Carr and Carr, 1980c), which have outer stomatal ledges which are not fused with the cuticle. The correct term for the aperture between the outer stomatal ledges is the *eisodial aperture*. The problems of stomatal breakthrough in the

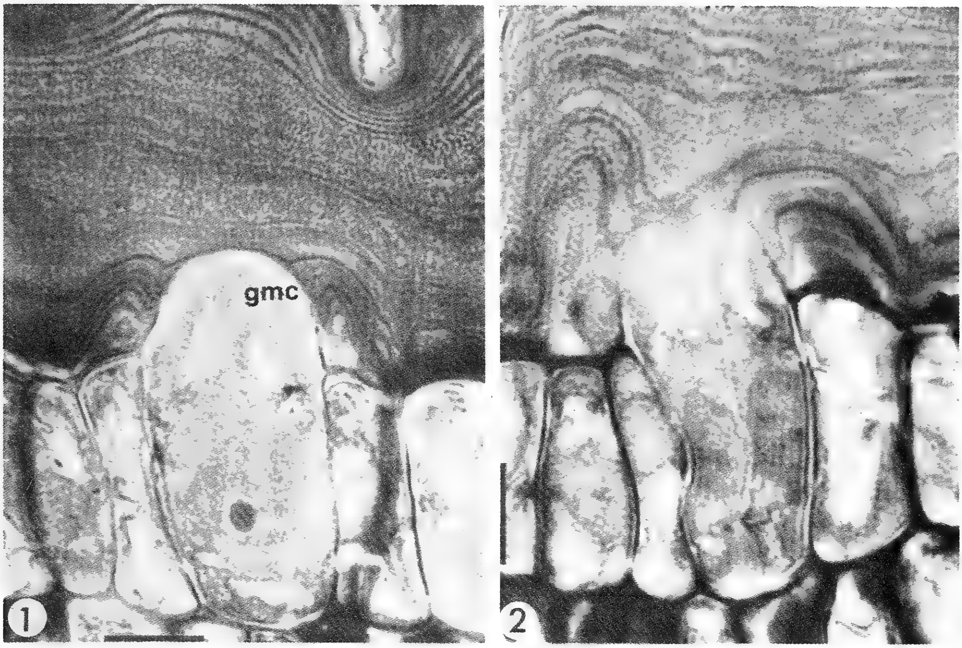


Fig. 5. Stomatal breakthrough, giant stomata. Developing leaf of *E. maculata*, abaxial surface. In **2** the guard mother cell (gmc) has divided, giving rise to the guard cell initials. Scale bar, 10μm.

Corymbosae are quite different from those we have observed in other eucalypts, or in common mesophytic plants such as *Phaseolus* and sunflower (Carr and Carr, in preparation), and are solved in quite a different manner, because of the presence of a layered, rubber cuticle above the stomatal complexes.

In the *Corymbosae*, the guard mother cell (GMC) expands and produces a vacuolate apical swelling or papilla which extends into the cuticle above it. As it touches the layers of rubber they appear to dissolve and their cut edges adhere to it (Fig. 5 [**1**]). The GMC divides anticlinally to yield the two guard cell initials (Fig. 5 [**2**]). Next the apical swelling relaxes so that the outer surface of the developing guard cells resumes a position level with the rest of the epidermal cells (Fig. 6 [**1**]). Still within the mother cell envelope, the two guard cells begin to lay down the layers of their upper and lower wall thickenings. These become cutinized (Fig. 6 [**2**]). They will eventually form the inner and (part of) the outer stomatal ledges. At this stage, above the developing guard cells a conical zone appears in the cuticle (Fig. 7). The zone is filled with a granular precipitate. It is evidently a region in which dissolution of the rubber layers takes place, the precipitate being, presumably, a product of the digestion of the rubber. A similar conical zone of dissolution has been reported by us as appearing above the developing guard cells of *Eucalyptus incrassata*, which has a thick *cutinized* (i.e. non-rubber) cuticle (Fig. 7 [**2**]). It is therefore timely to give such a zone a name; we have called it the *conus*, short for *conus dissolutionis*. Our interpretation of the origin of the conus is that the guard cells, still enclosed within their mother cell envelope, secrete into the cuticle enzymes capable of digesting the cuticle, whether it consists of rubber (as in the *Corymbosae*) or of cutinized layers. Very probably the GMC itself has some of the necessary enzyme (we may call it a

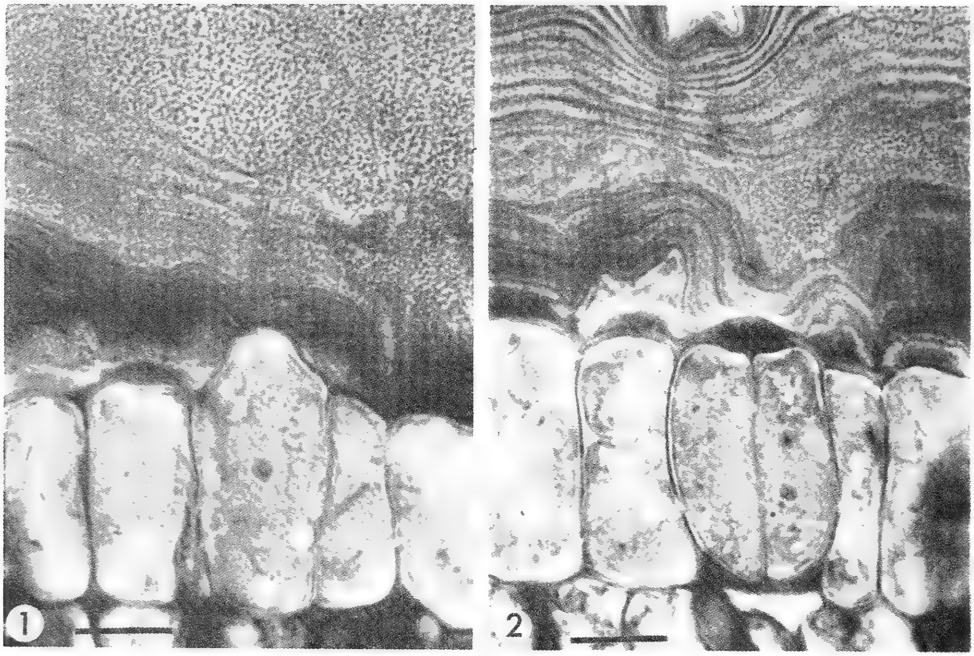


Fig. 6. As Fig. 5, to show later events in stomatal breakthrough. In **1** the guard cell initials have withdrawn dragging with them the innermost rubber lamellae. **2**, upper and lower guard cell thickenings have begun to form inside the old gmc envelope.

'*laticase*' in the *Corymbosae*) on its outer surface and that this is the reason for its ability to break through and attach to itself the rubber layers it touches.

As the conus enlarges and the number of still undigested rubber layers above it decreases, it begins to intersect with the outermost layers of rubber. At this stage, scanning electron microscopy of the leaf surface (Fig. 8 [**1**]) shows a number of black annuli (black because the thin cuticle is not as electron-reflective as elsewhere). Within such an annulus a circular line of breakage appears and the inner disc of rubber is released, shrivels and is lost (Fig. 8 [**2**]; Fig. 10 [**4,5,6**]). A more-or-less circular opening is left in the cuticle, leading down, through similar jagged holes in successive layers, to the guard cells. Inverted cuticles show these layers and the jagged edges of the holes made in them Fig. 8 [**6**]). This method of stomatal breakthrough applies to the earliest stomata formed on the leaf. These stomata, because they have an unusually high complement of subsidiary cells, are referred to as *giant stomata.* We shall have more to say about them in the second part of this lecture.

Stomata formed later on, when the cuticle is rapidly thinning, also each have a conus but it becomes stretched out by the lateral expansion of the cells of the stomatal complex and is shallow (Fig. 9 [**2**]). Where it intersects with the surface layers of the cuticle it presents more the appearance of a small dot or a line (Fig. 11 [**3,4,5**]). Cracks appear along such a line and join up to form a slit. No disc of rubber is released. As leaf expansion continues, the slit widens to become an ellipse (Fig. 11 [**8,9**]), often still showing at its ends the traces of the line which initiated it. Inverted cuticles show the shallow cavities in the cuticle, above the ordinary stomata (Fig. 8 [**5**]). Breakthrough in these ordinary stomata brings the outer thickenings of the guard cells in contact with the outermost layers of rubber (Fig. 9 [**4**]) and they fuse with them to form a composite *outer*

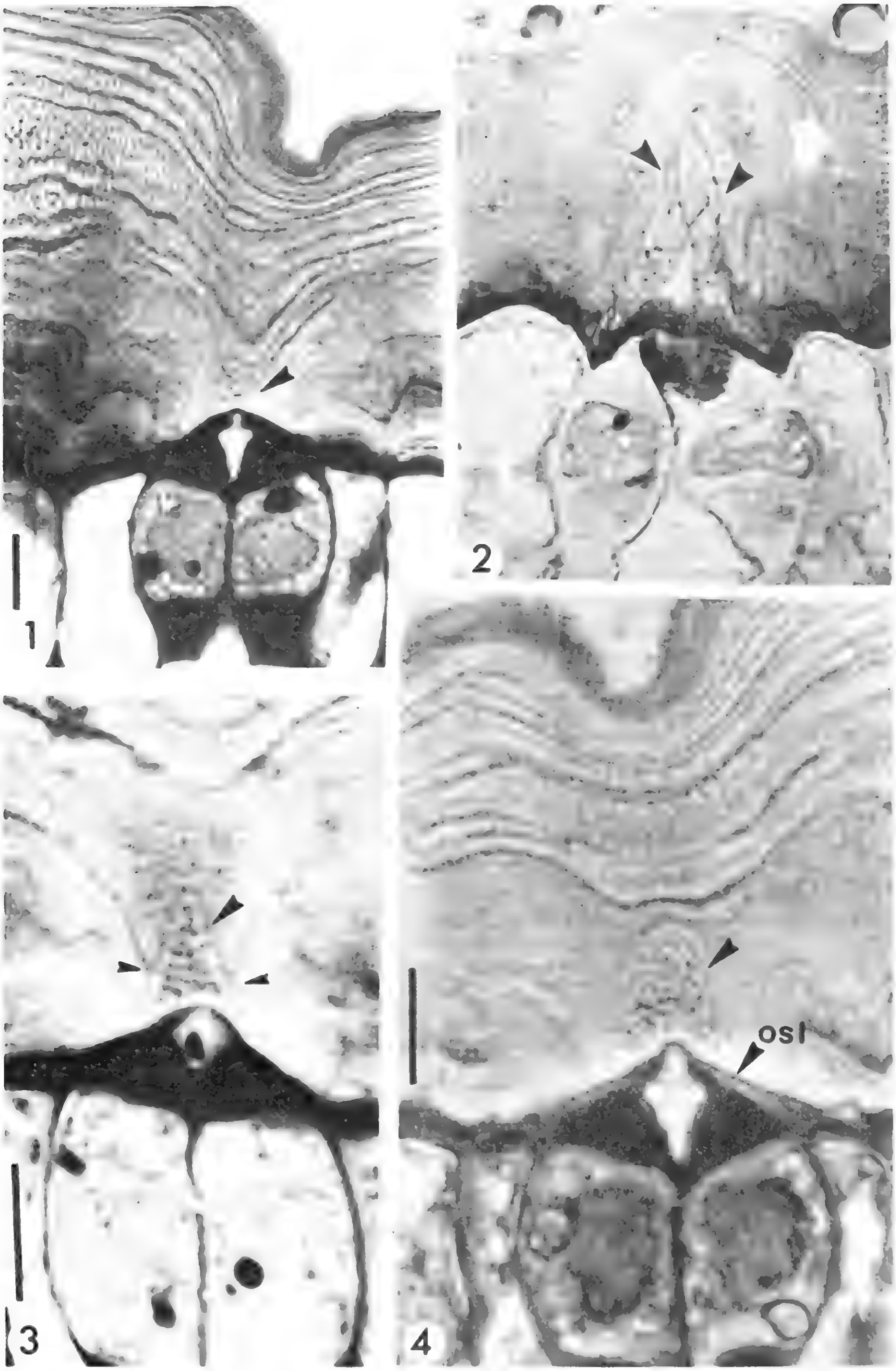


Fig. 7. All except **2** *E. maculata*, to show the initiation of the *conus dissolutionis* (arrowheads) outside the gmc envelope. osl, outer stomatal ledge. **2**. The conus (arrows) above a developing stoma of *Eucalyptus incrassata*. White arrowhead (**2**), layering of the cuticularized cuticle. Scale bars, 10μ.

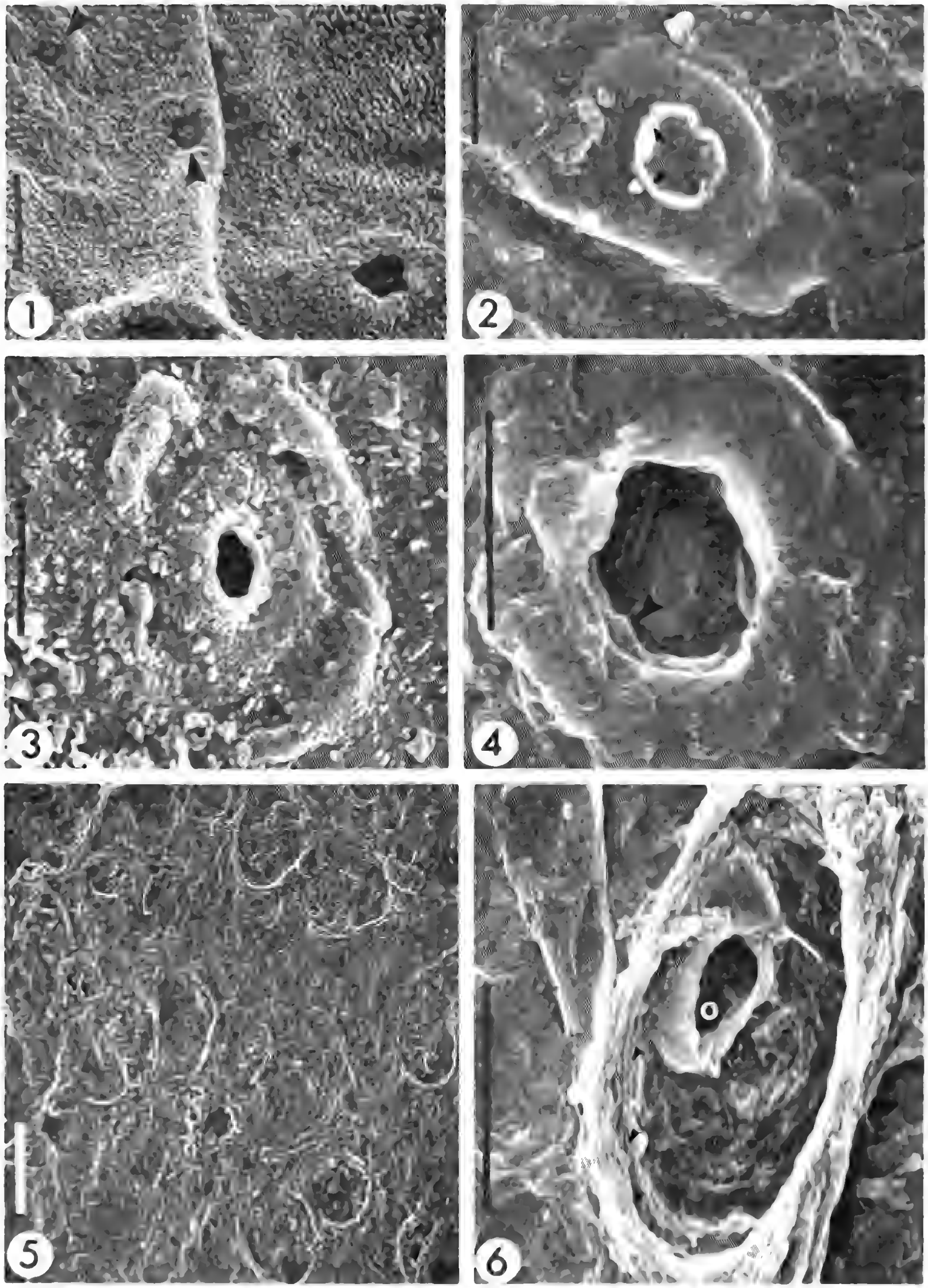


Fig. 8. Stomatal breakthrough, scanning electronmicrographs *E. erythrophloia*. **1**. Arrows, dark circles indicating imminent breakthrough. **2**. Detachment of the rubber disk, split appearing between two thickened rims of the annulus. **3**. Breakthrough completed and peristomatal cuticular ornamentation beginning to form. **4**. Through the ostiole, lamellae of the cuticle can be seen. **5** and **6**. Detached, inverted cuticle taken from a leaf at a late stage in stoma formation. Cup-shaped hollows in the cuticle where stomatal breakthrough has occurred or is occurring. **6**. One such area enlarged. Small arrowheads indicate lamellae in the cuticle. o, ostiole. Scale bars, all 10μm.

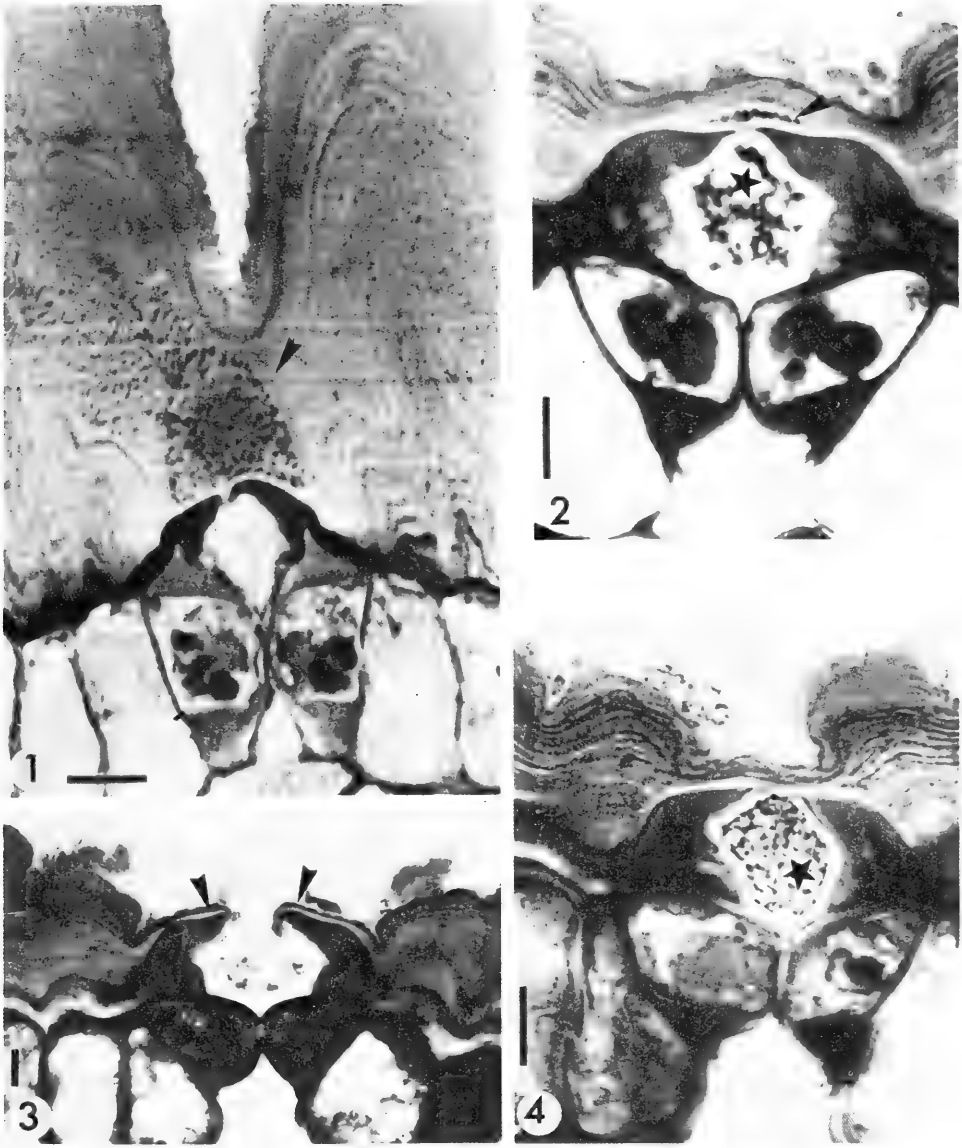


Fig. 9. E. maculata, completion of stomatal breakthrough. **1**. Large conus (arrow) of 'giant' stoma touching the outer surface of the cuticle. **2**. Small, flattened conus of 'ordinary' stoma. Guard cells almost fully formed. **3**. Completed ordinary stoma. Outer stomatal ledges formed as a composite of the guard cell thickenings and the outermost rubber layers. **4**. 'Ordinary' stoma about to break through to surface. Asterisks in **2** and **4** indicate accumulation in anterior chamber of stoma of breakdown products of the dissolution of rubber lamellae. Scale bars, all 10μm.

stomatal ledge (Fig. 9 [**3**]). Occasionally there is a developmental hiatus, in which the final breakthrough does not take place (Fig. 11 [**7**]). The stomata, although otherwise fully-formed, are 'blind', i.e. have no opening or *ostiole* on the surface, and are therefore clearly non-functional.

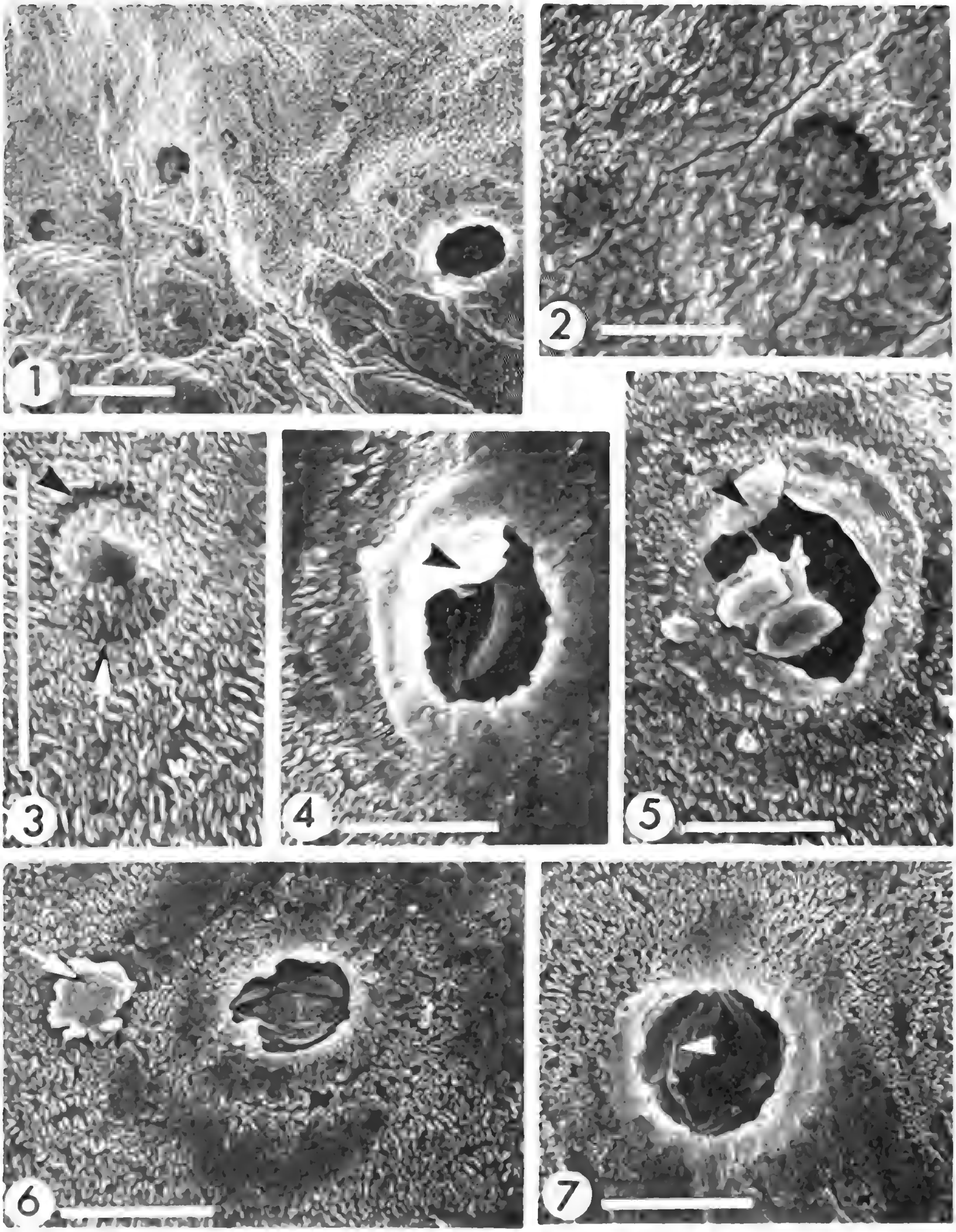


Fig. 10. Stomatal breakthrough, scanning electronmicrographs. *E. calophylla.* **1** and **2** dark rings, surrounding circular disks. **3**. Arrows indicate splitting of the circular disk from the rest of the (wax-covered) surface. **4**, **5**. Arrows indicate shrivelled disks still attached to the ostiole or **6** loose on the surface of the cuticle. **7**. Completed ostiole, through which one can observe (arrow) some of the lamellae of the cuticle. Scale bars, **1** 10µm; all to same magnification.

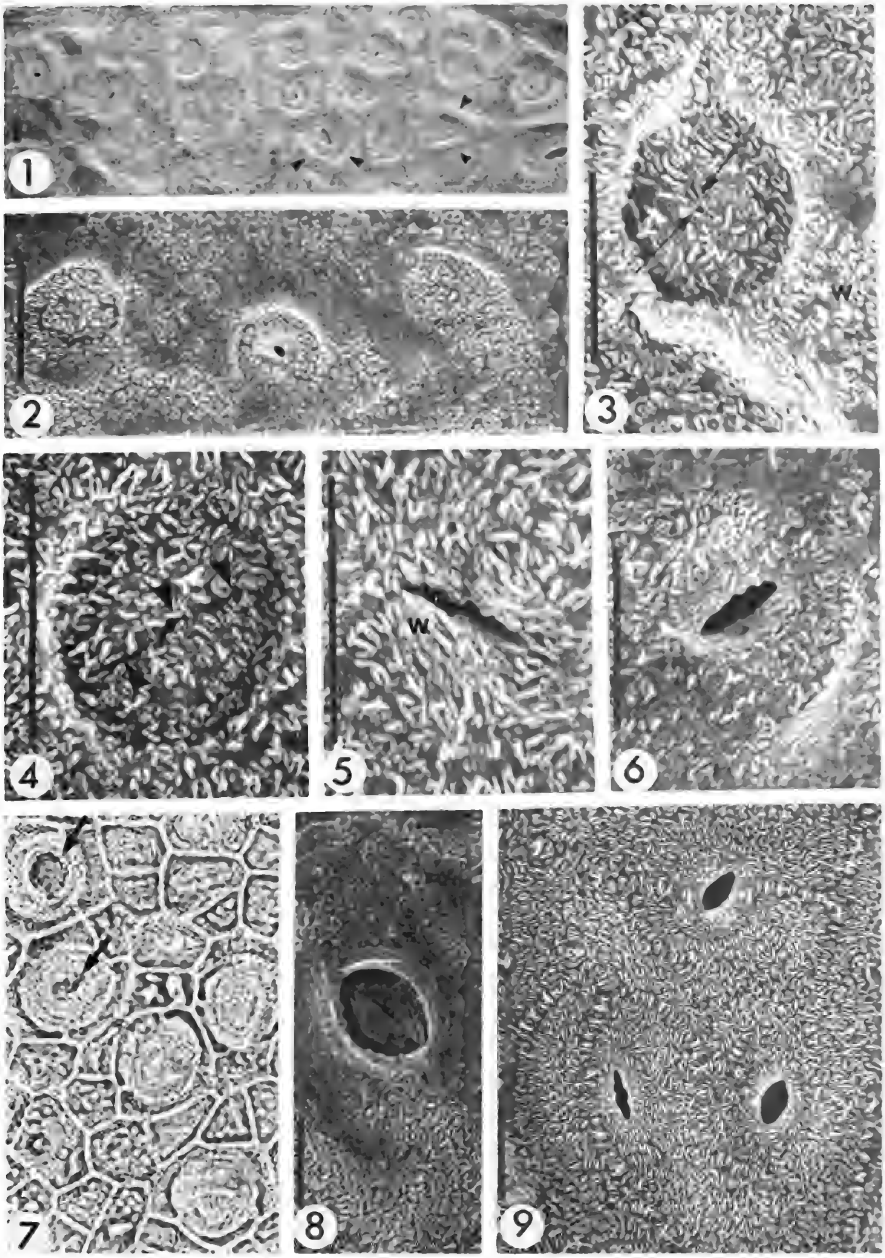


Fig. 11. Stomatal breakthrough of 'ordinary' stomata. Scanning electronmicrographs. **1-8**, *E. calophylla*, abaxial surface. **1** and **2**. A field of stomata developing and breaking through. Note that the peristomatal cuticular ornamentation has begun to form (arrowheads). **3-6**. Breakthrough beginning as a slit or crack (arrows) in the outer surface and **6** the ostiole completed. W, wax crystallites. **7**. Light micrograph of leaf surface of a specimen of *E. hamersleyana*, showing (arrows) stomata with ostioles; the other stomata have no ostioles and are non-functional ('blind'). **8**. *E. calophylla*. After breakthrough, the ostiole enlarges and becomes elliptical. In **8** the outer stomatal ledges are visible through the ostiole. **9**. *E. eremaea*. Fully-formed 'ordinary' stomata. Scale bars, all $10\mu m$.

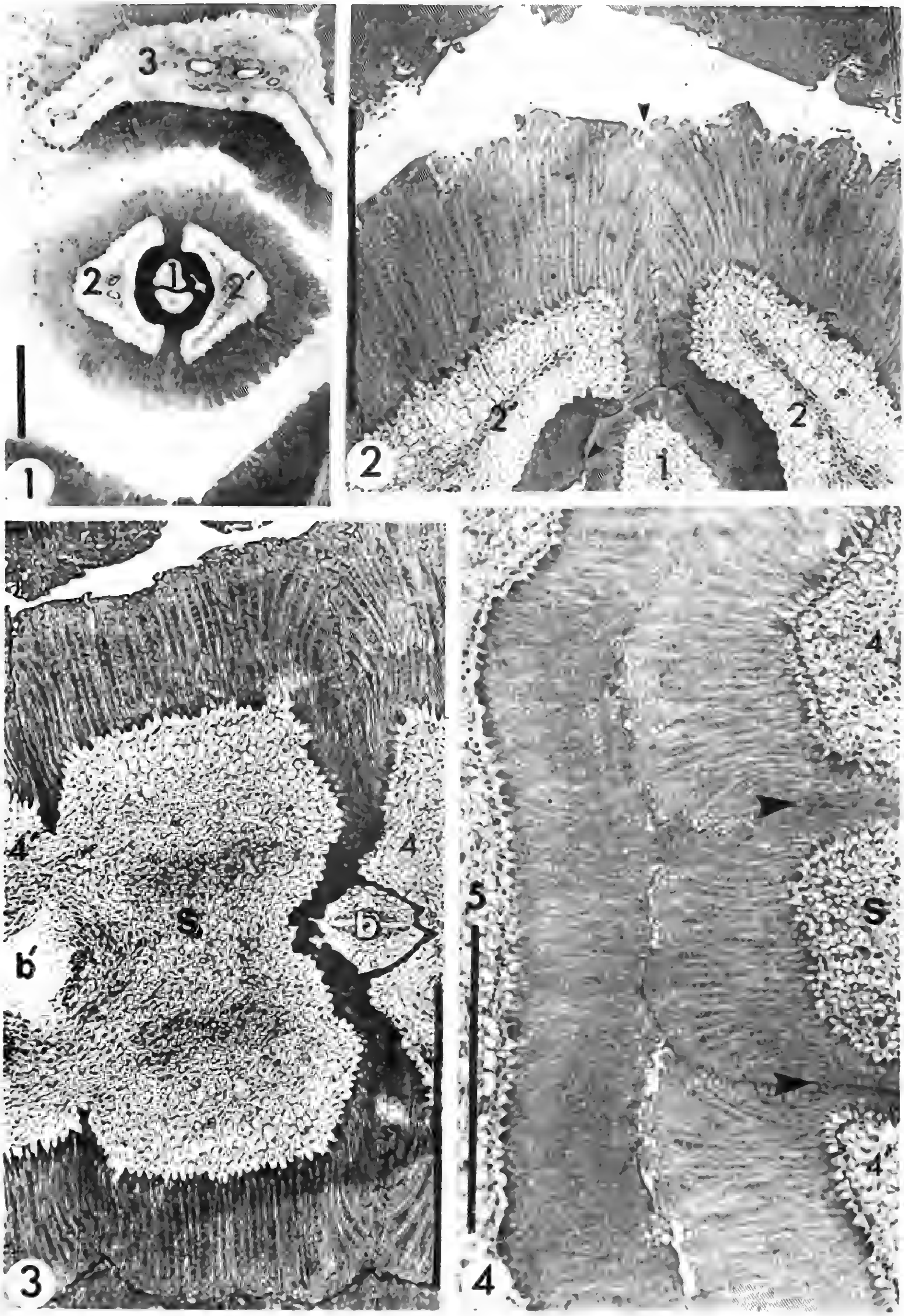


Fig. 12. Transverse sections of a leafy bud of *E. collina*. **1-5** transverse sections, **1** and **2** near the tip of the bud, **3** and **4** near its base. The leaf primordia are numbered in basipetal sequence, the precocious primordium of a pair with a prime (as e.g. 2′). b, b′, axillary buds (or, in b′, a position above an axillary bud), S, stem. Arrowheads indicate positions where the cuticle of one primordium abuts on that of another. Scale bars, **1** 1mm, all the others 10μm.

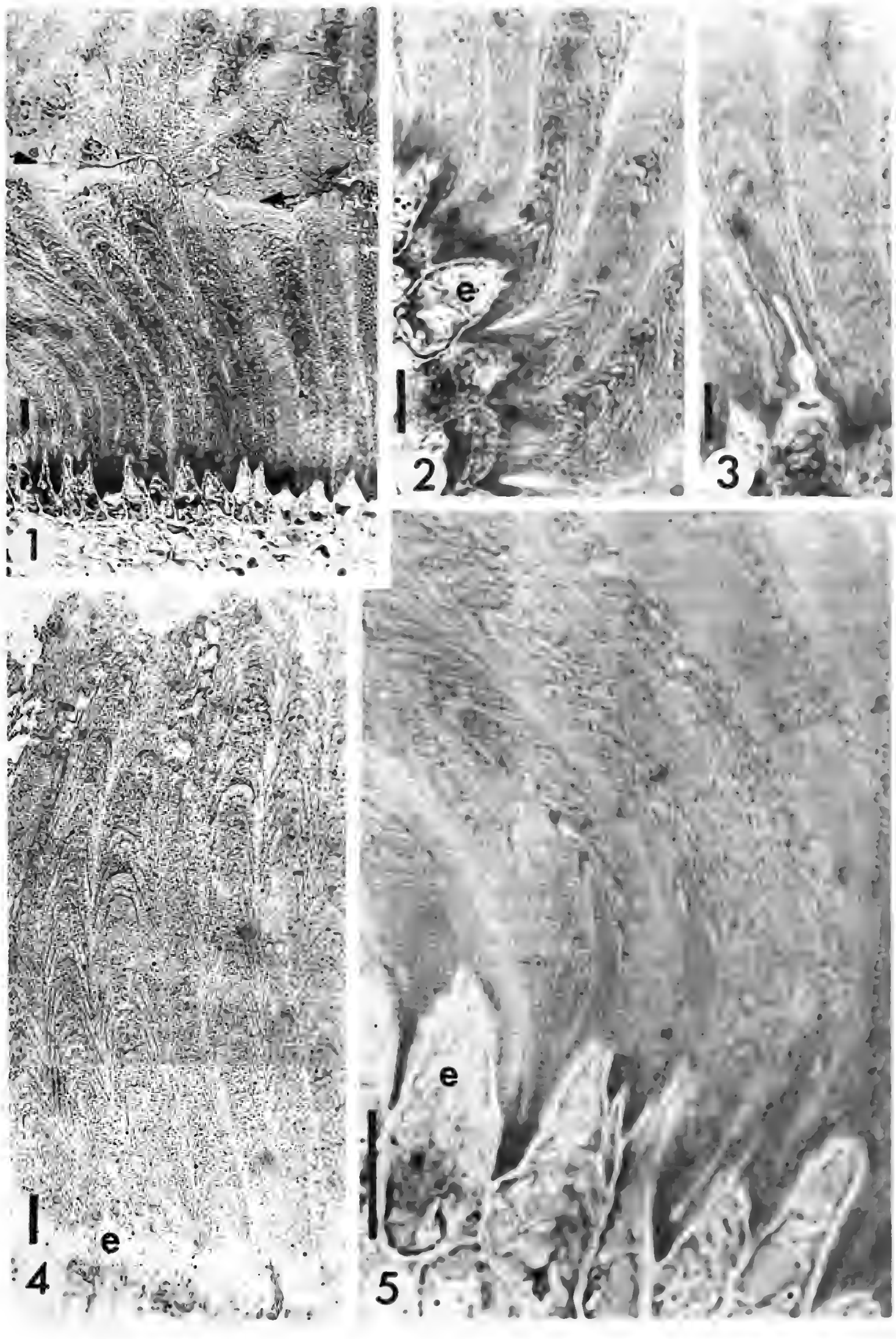


Fig. 13. E. collina; details of epidermal cells and cuticle lamellae. e, epidermal cell. In **1** arrows indicate abutment of cuticle of one primordium on that of another. Scale bars, all 100μm.

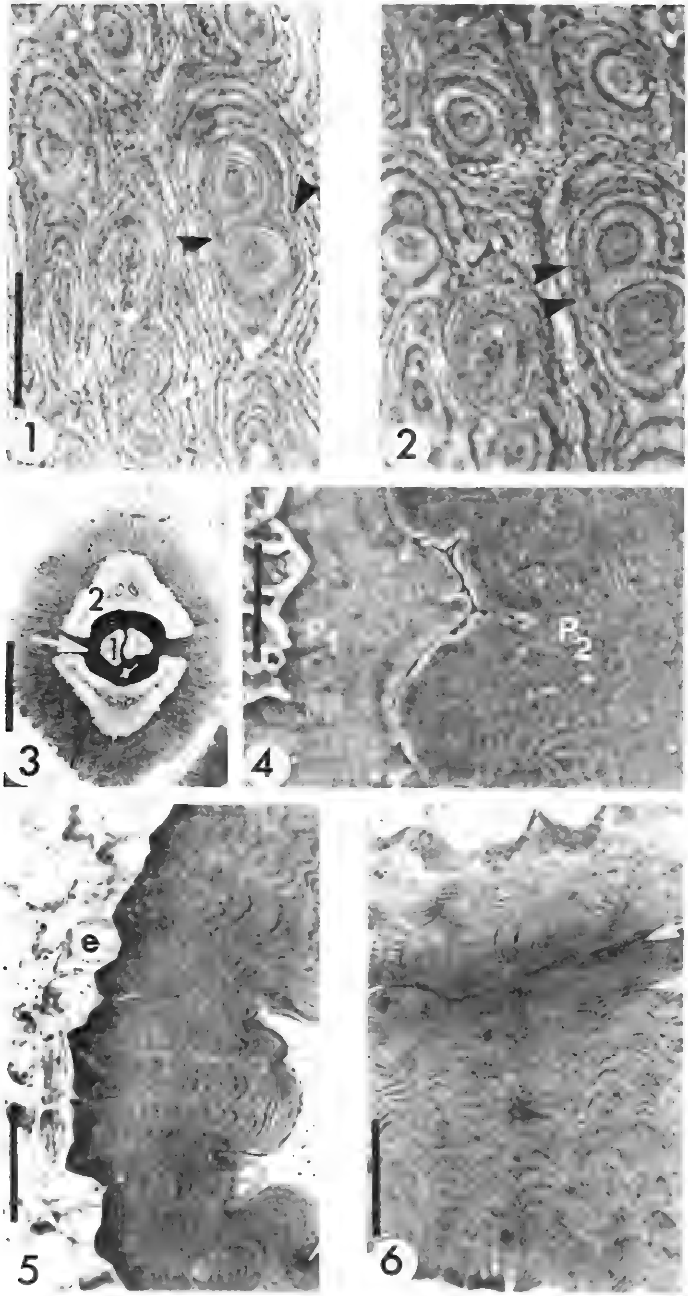


Fig. 14. E. collina, cuticle. **1** and **2**. Tangential sections of cuticle showing concentric sections of domes of the cuticle over individual cells. Arrowheads show the envelope of a single cell, now divided to give two cells. **3-6**. Transverse sections to show the adaxial cuticle (arrow in **1**) of leaf primordia (numbered as before). The layers of cuticle are much more compact and consequently less domed than those of the abaxial surface. These less wavy layers are maintained as the outer layers of the adaxial surface on an older primordium **6**. e, epidermal cell (its surface noticeably less ridged than those of the abaxial surface). Scale bars, **3** 1mm, all the others 100μm.

In our recently-published book, *Eucalyptus II*, we have given a full account of these methods of stomatal breakthrough in the *Corymbosae*. We have also dealt with a third and quite different method, which is that followed by stomata initiated on the outer surface of the flower buds, as well as on the outer (abaxial) surface of the petals.

Scurfiness of the cuticle

Among the other consequences of the presence of a layered, rubber cuticle in the *Corymbosae*, is the possibility of *scurfiness* of the cuticular surface. Glaucousness in eucalypts is due to coverings of epicuticular wax in the form of tubes on the surface of leaves or flower buds. No species of the *Corymbosae* have tubular wax; those which have epicuticular wax have it in the form of wax platelets. It follows that none of the species of the *Corymbosae* can be glaucous. However the flower buds and, in a few cases, the young leaves of some species have a silvery sheen, usually described as *scurfiness*. The origin of scurfiness is explicable in terms of the layered cuticles of the *Corymbosae*.

For its investigation, we have used a herbarium specimen of the tropical Western Australian species, *E. collina*. Fitzgerald, who discovered this species wrote of it that the branchlets and often the leaves appear 'as if covered with frost'. 'The trees can be seen at a great distance, owing to their silvery whiteness, which is a distinct character of the plant'. Dissections and transverse sections of leafy buds show that scurfiness is already apparent on the surface of the second smallest leaf primordia (P_2) and increases during the maturation of the leaves. After that, much of the scurfiness is gradually lost from the leaf surface, remaining, in the fully-developed leaves, mainly on the midrib and petiole. The innermost leaf primordia in the bud are tightly packed together forming what appears to be a solid mass, enclosed by the leaf cuticles (Fig. 12 [**1**]). For reasons we have already explained, and resulting from the close apposition of the adaxial surfaces of the innermost primordia, the abaxial cuticles become much thicker (at least initially) than the adaxial cuticles. The cuticle is strikingly layered, in much the same way as the cuticle of *E. maculata* (Fig. 13). On a P_4 leaf primordium, one can count 32 to 35 layers of the cuticle (Fig. 13 [**4**]). As in *E. maculata*, this suggests again a bilayer produced every day, assuming a plastochrone (interval between the production of successive leaf primordia) of about 8 days.

Each layer consists of a series of domes, each produced over a single epidermal cell (Fig. 13 [**1,2,5**]). Each of these domes joins laterally with those of adjacent cells to form an undulating layer (Fig. 14 [**4,5,6**]). Cut tangentially (Fig. 14 [**1,2**]), the cuticle presents the appearance of a series of concentric circles, the domes of individual cells cut at various levels. Where a cell has divided, these circles are enclosed in ellipses representing the now expanded and distorted domes of the original cell.

Scurfiness appears as outermost layers begin to break down and exfoliate (Fig. 15). The outer layers appear to become too brittle to stretch to accommodate the continued expansion to the surface of the leaf primordium. Possibly the rubber oxidizes prematurely and loses elasticity. Cracks appear in the domes (Fig. 15 [**2,3**]) and the cracks spread, allowing rafts of detached cuticle to form (Fig. 15 [**4**]). Spaces between the detached cuticular layers fill with air, the source of the silvery sheen of the scurfy cuticle.

Scurfiness of flower buds also arises from breakdown of the outer layers of rubber cuticle, as is discussed and illustrated in *Eucalyptus II*. Deep fissures develop in the cuticle and rafts of the outer layers may exfoliate.

Discussion

Following its initiation, the GMC ceases to form rubber. Indeed, its outer surface may be coated with a laticase. We had already shown for other eucalypts (not *Corymbosae*)

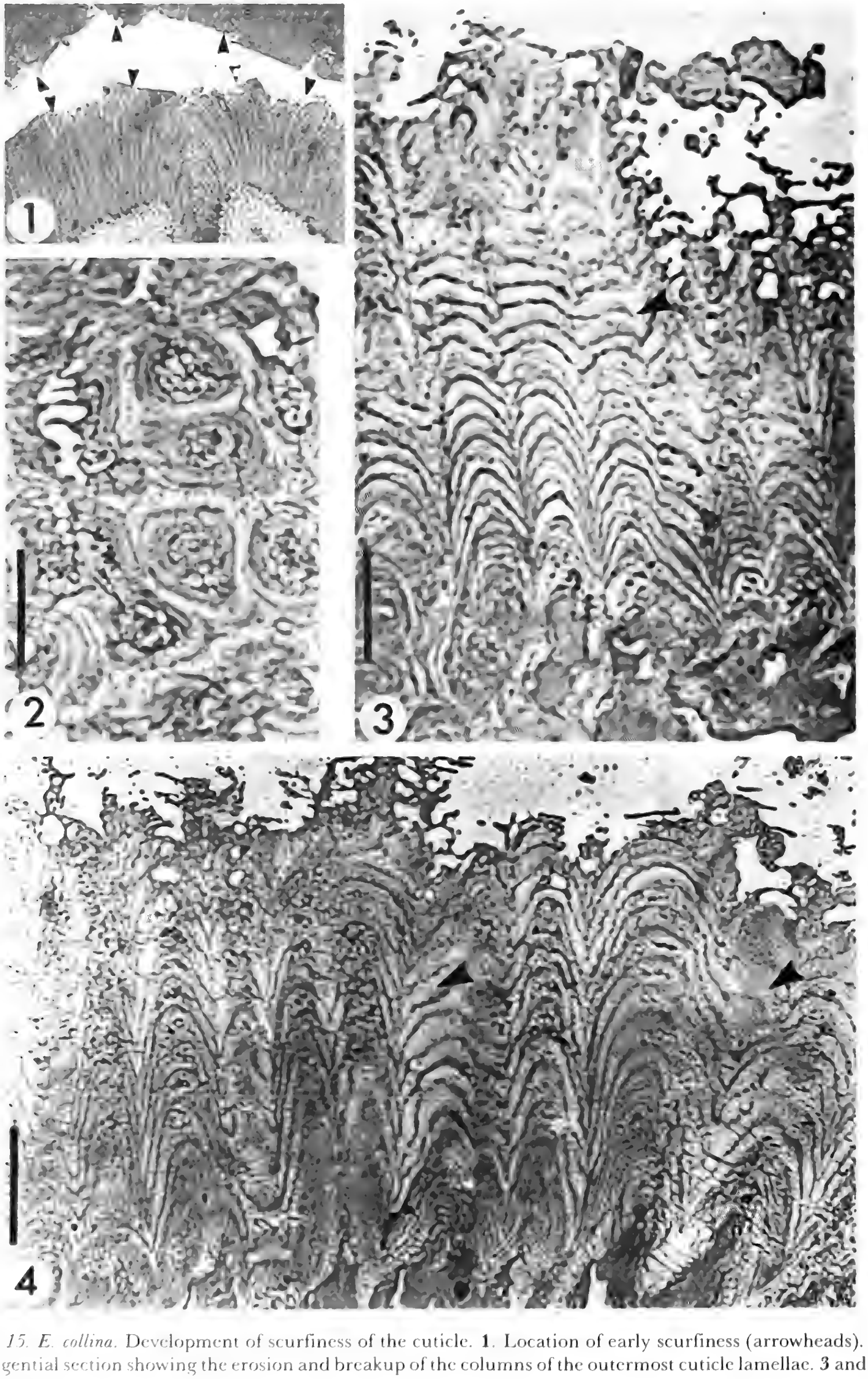


Fig. 15. E. collina. Development of scurfiness of the cuticle. **1**. Location of early scurfiness (arrowheads). **2**. Tangential section showing the erosion and breakup of the columns of the outermost cuticle lamellae. **3** and **4**. Swelling of the light zones (arrowheads) and breakaway of the outer layers. Scale bars, **1** 1mm, all the others 100μm.

that, following its initiation, the GMC ceases to make cuticle above itself (Carr and Carr, 1978). Next, the guard cell initials which result from the division of the GMC begin to produce cuticularized layers within the mother cell envelope. The sequence of production first, of rubber layers, then of cuticularized layers of the cuticle is also that followed by the ordinary cells of the epidermis. This dual potentiality may have been a feature initially common to the ancestors of all the eucalypts but the capacity to produce rubber was reduced or lost in most groups of eucalypts. In some species perhaps only a few of the outermost layers of the cuticle consist of rubber (giving the cuticle a characteristic sheen) while the bulk of the cuticle consists of cuticularized layers. A rather similar situation is found developmentally in the leaves of certain deciduous species of the *Corymbosae* in the tropics. Following a few weeks of leaflessness, a new suite of thin, pale green leaves is produced which expand rapidly over a few days then gradually become thicker and darker green. In such leaves the initial cuticle of rubber is relatively thin and paucilamellate and, following the attainment of full size, a relatively thick cuticularized cuticle is developed to reinforce the protective layers. On this hypothesis, the rubber cuticle of the *Corymbosae* represents the survival of an ancient device for the protection of the leaf during its early expansion. This has given way, in most species of eucalypts, to the production of the less-overtly layered, cuticularized cuticles which are also a feature of most angiosperms.

The flower is considered by morphologists to be a 'conservative' organ in relation to evolution. In the flowers of the *Corymbosae* only a rubber cuticle, which is in many instances remarkably thick and is always layered like that of the leaves, is formed. This supports the hypothesis that the rubber cuticle is, in an evolutionary sense, an older covering than the cuticularized layers. One can visualize that a rubber cuticle would present advantages to tropical species which, either deciduous or semi-deciduous, must rapidly expand a suite of leaves while still retaining a protective cuticle over their surfaces. Unfortunately we know little about the cuticles of tropical plants, but it seems not unlikely that rubber cuticles may be found to be present in genera other than *Eucalyptus* and *Angophora*.

A host of questions is raised by these findings. Are the bilayers really diurnally produced, and if so which of the two constituent layers is produced during the day and which during the night? Is layering suppressed in continuous light, as it is in insect cuticles and the cell walls of cotton hairs? Why are the cuticles of some species and some organs scurfy, those of other species and other organs not? Is the eventual hardening of the initially elastic cuticle due to oxidation, as was suggested by Smith (1908)? Perhaps scurfy cuticles lack antioxidants, such as α-tocopherol, a known constituent of eucalyptus oil; alternatively, since scurfy cuticles lack epicuticular wax, perhaps it is this lack which permits the development of scurfiness.

Qualitative and quantitative aspects of the phytoglyph in *Corymbosae*

In 1883 Ferdinand von Mueller wrote, concerning the plant fossils found in association with the deep leads of the Victorian goldfields, that: 'By the aid of the microscope we may yet hope to be able to obtain characteristics of diagnostic value from the anatomy of leaves sufficiently positive to recognize ordinal and even perhaps generic groups'. 'How far this can be done even with living plants remains yet to be studied: but I was enabled, for instance, to demonstrate the occurrence of Epacridae in New Guinea from the microscopic comparison of the leaf epidermis, brought from thence without flowers or fruits, with the very peculiar cuticle of many Epacridae easily recognized microscopically'. In his *Eucalyptographia* Mueller illustrated features of the leaf epidermis of 39 species of eucalypts. He classified them as *isogenous*, with roughly equal numbers of

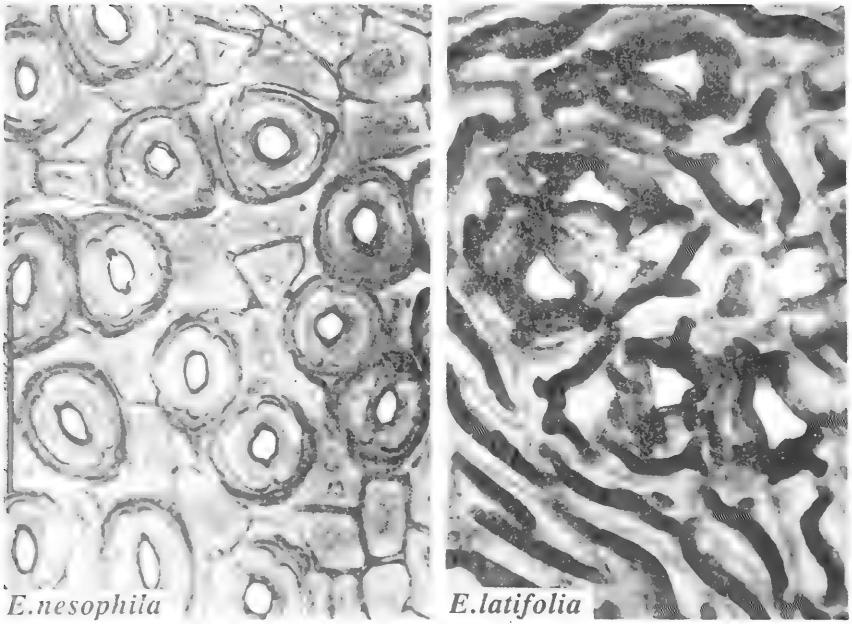


Fig. 16. E. nesophila and *E. latifolia*, showing different patterns of cuticular ornamentation. (Figs 16-23 all light micrographs of stained cuticles; in comparisons always the same surface, upper or lower of the two species, at the same magnification is shown.) Scale bar: 50μm.

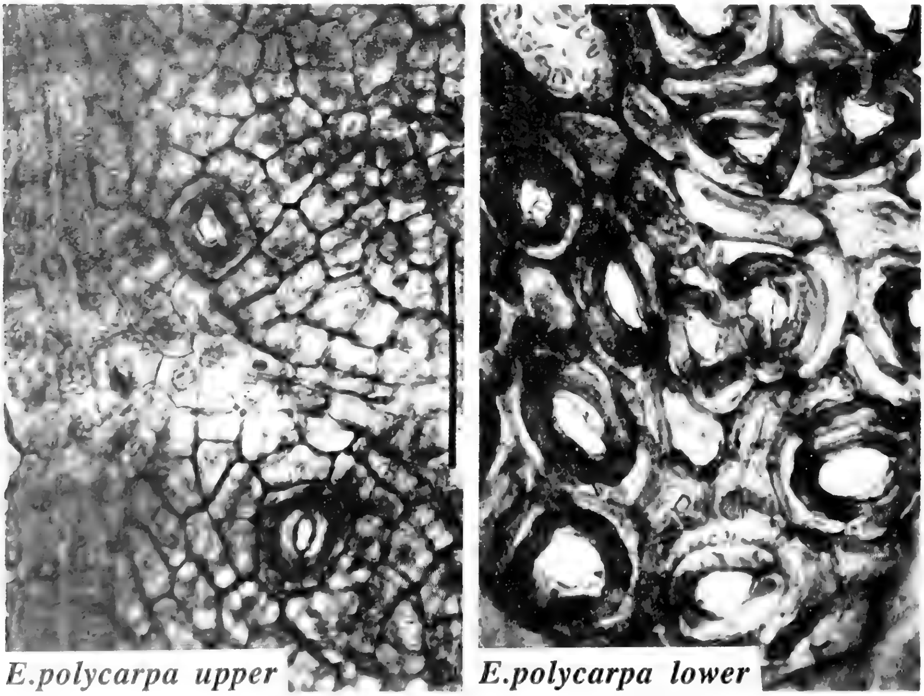


Fig. 17. E. polycarpa, showing heterogenous arrangement of the stomata. Scale bar: 50μm. See also legend to Fig. 16.

stomata on both upper and lower surfaces, *heterogenous*, with many fewer on the upper than on the lower, or *hypogenous*, with stomata only on the lower surface.

This excellent beginning of the study of the microscopic features of the leaves of Australian plants suffered a mortal blow when Maiden (1909-1928), after quoting Mueller's stomatal classification, dismissed the study of stomata with the remark (our emphasis) that '*the method cannot be used for diagnostic purposes because of the variation in the distribution of stomata even in the same tree*'. Maiden offered no evidence of such variation and indeed made no further reference to stomata in his voluminous writings. Since that time no-one paid any attention to the features of the epidermis of eucalypt leaves until, in 1971, we published an account of our studies (Carr *et al.*, 1971) of the leaves of the various 'type materials' supposed by Blake (1953) to be all of a single species, *Eucalyptus dichromophloia*. We were able to demonstrate that these materials belonged to no fewer than five different species. Blake had based his description of the juvenile foliage of *E. dichromophloia* on leaves of a species of *Angophora*, included in the folders of one of these species of eucalypts. Recently, in our new book, *Eucalyptus II*, we have shown that the type folders of *E. erythrophloia* (which included the *Angophora* leaves) also contain a specimen of leaves of yet another species (*E. ellipsoidea*), which is described for the first time. Thus the type folders of *E. erythrophloia* contain specimens, all collected in the same locality (where they still occur), of no fewer than three species belonging to two genera! The methods we used included scanning electron microscopy of the leaf cuticles, and light microscopy of stained cuticle preparations and of thin sections of cuticles. These approaches make it possible to reconstruct a 3-dimensional view of the cuticular patterns of the leaves and an analysis of the positions, shapes and types of cells in the leaf epidermis. For the totality of the information thus obtained we coined the term '*phytoglyph*', which means literally 'plant fingerprint'. We maintain that, just as human fingerprints may be used diagnostically to identify persons, so the phytoglyph may be used to identify species of eucalypts, at least in some groups.

Following the work on '*E. dichromophloia*', we used the method to identify old specimens, collected by Leonard Brass in Cape York Peninsula (and which had been filed under *E. dichromophloia*) as *E. nesophila* (S.G.M. Carr, 1972). At that time, this species was thought to be endemic to the Northern Territory. Dr Nigel Wace then presented us with a problem in the form of a small leafy shoot collected on Fenelon Island, off the coast of South Australia. We identified the material as belonging either to *E. socialis* or to a closely related, possibly undescribed, species (Carr and Carr, 1976). At about the same time, that species, *E. yalatensis*, was described by C. D. Boomsma. Our further studies showed that the species of the informal group, the *Bisectae*, have several peculiarities of the leaf cuticle. In some species, during stomatal breakthrough, the cuticle becomes eroded into sinuous canyons or crypts, at the bottom of which lie groups of stomata (Carr and Carr, 1978, 1980b, 1980c). Other species of the *Bisectae* have special bars of cuticle forming the line of closure of the stomata (Carr and Carr, 1979). Yet others have peculiar ingrowths of cuticle in the anterior chambers of the stomata (Carr and Carr, 1980a). These features of the *Bisectae* were shown to be consistent with taxonomic relationships within that group. While such studies showed the usefulness of phytoglyphic methods, but by far the most successful and extensive use we have made of those methods has been in clearing up what M. R. Jacobs termed 'the bloodwood puzzle', i.e. the problem posed by the recognition and identification of the confusing and numerous tropical species of the *Corymbosae*. We have published accounts of these species in our two books, *Eucalyptus I* and *Eucalyptus II*. In doing so we refrained from adding to the volume of descriptive data by including all the data from the immensely detailed phytoglyphic studies which largely enabled us to sort the hundreds of available specimens into groups which formed the basis of species descriptions.

In what follows we now provide a resume of the sorts of information which can be obtained from phytoglyphic studies of the *Corymbosae* and which can be used as aids to species identification. All the photographic illustrations are light micrographs of stained leaf cuticles.

Qualitative features of the leaf epidermis in *Corymbosae*

A wide variety of phytoglyphic features is shown by different species of the *Corymbosae*. The cuticular ornamentation of the subsidiary cells of the stomata may be very simple, as it is in the Eximiae (or yellow bloodwoods) and in, e.g. *E. nesophila*, or it may be very complex, as in e.g. *E. latifolia* and *E. capricornia* (Fig. 16). The ordinary, non-stomatal cells may contribute to the pattern of ornamentation (as they do in *E. latifolia*) or have little or no ornamentation. The illustration of *E. latifolia* was made from a specimen of that species from Papua-New Guinea, and the pattern matches exactly that of specimens from Australia. Similarly the illustration of *E. nesophila* is from a specimen from Cape York Peninsula and the ornamentation is exactly the same as that of specimens from the Northern Territory and Western Australia. The pattern is a constant feature of the species and within limits, does not vary over the entire range of the species or in cultivation. Moreover, it is constant over time, so that specimens collected during the last two centuries may be compared and identified with recently-collected specimens.

As Mueller was aware, some eucalypts have no stomata on the upper surface of the leaf, or may have many fewer stomata on the upper surface than on the lower. Contrary to what Maiden wrote, these are constant characteristics for the species. For instance, *E. polycarpa* has scattered stomata on the upper surface of the leaf with a stomatal density of about 1 per square millimetre (Fig. 17), except near the margins and midrib where the density is about 3 per square millimetre. (Other, related species, have either no stomata on the upper surface or higher densities of stomata than *E. polycarpa*).

The cap cells of oil glands have rather thin, unornamented cuticles. In the *Corymbosae* they are arranged in characteristic groups of 3 or more per oil gland and so are easily recognized in the light microscope. Some species, such as *E. terminalis* have large numbers of groups of cap cells on both sides of the leaf; others (e.g. *E. ollaris*, *E. opaca*) have few or none (Fig. 18). There may be differences between upper and lower surfaces. For instance *E. polycarpa* has very few such groups on the upper surface, but large numbers on the lower surface. Similarly the actinocytic 'giant stomata' may be less common on the upper surface than on the lower; some species (e.g. *E. opaca*, *E. centralis*) have relatively few giant stomata on either surface of the leaf, while other species (e.g. *E. terminalis*) have many on both surfaces. We shall make further reference later on to 'giant stomata'. Finally, the stomata of some species are in general larger than those of other species (Fig. 19).

If studies of macroscopic morphology such as fruit shape and size, features of the flower, leaf shape and arrangement etc. suggest that two specimens are of the same species, we may expect that their phytoglyphic features will be identical. In *Eucalyptus II* we have shown that the specimens which (wrongly) have been called *E. perfoliata* have features of the flowers which are identical with those of *E. lamprocalyx*. The fact that the phytoglyphic features of these specimens are identical with those of *E. lamprocalyx* (Fig. 20) supports the hypothesis of identity, and since the only validly-published name is that of *E. lamprocalyx*, it is under that name that we must now file specimens previously termed '*E. perfoliata*'.

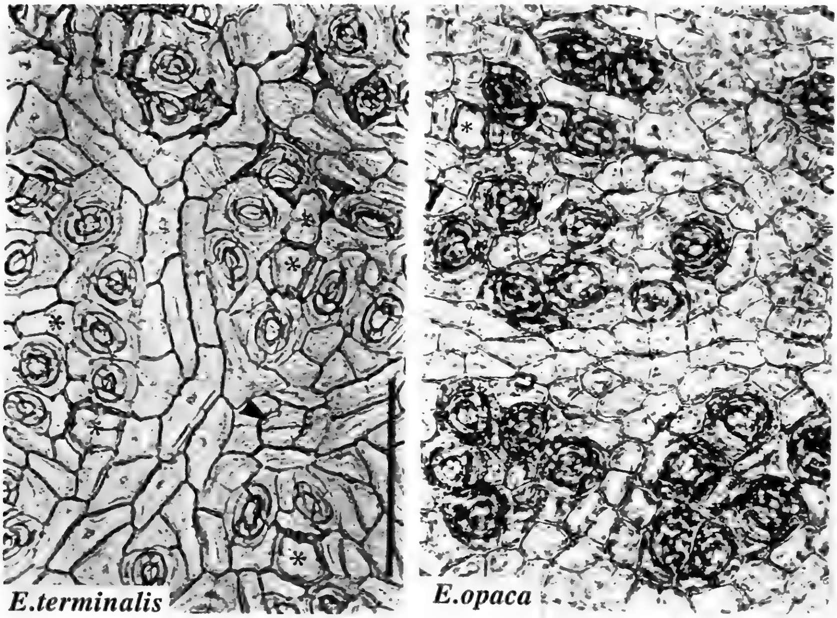


Fig. 18. E. terminalis, with many groups of oil gland cap cells (asterisks) and *E. opaca* with only one. Arrowhead, giant stoma of *E. terminalis*. Scale bar: 500μm. See also legend to Fig. 16.

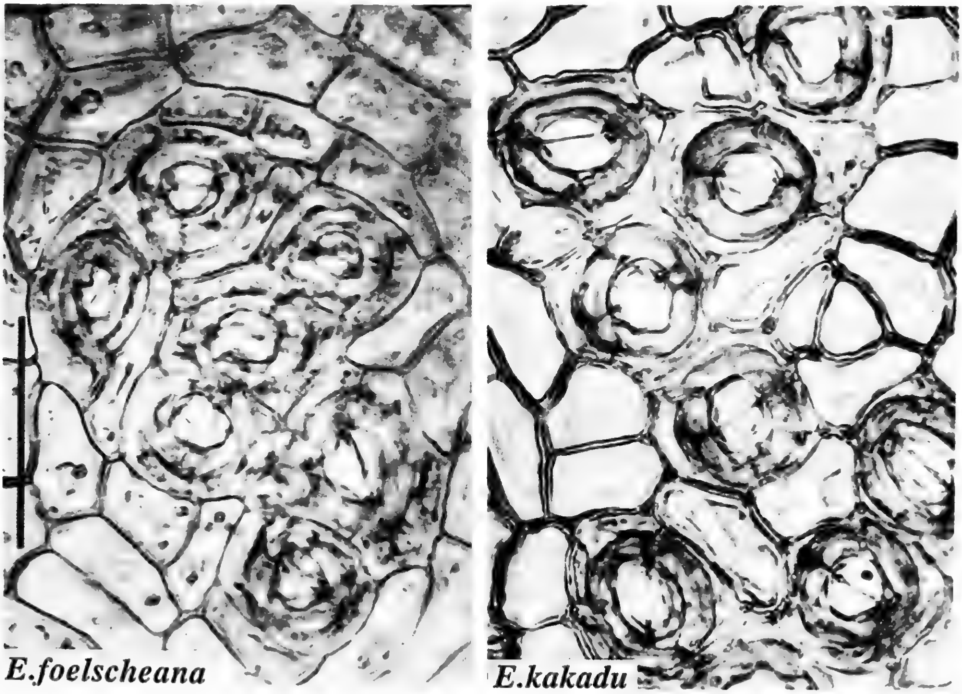


Fig. 19. E. foelscheana and *E. kakadu*, to show differences in size of stomata. Scale bar: 50μm. See also legend to Fig. 16.

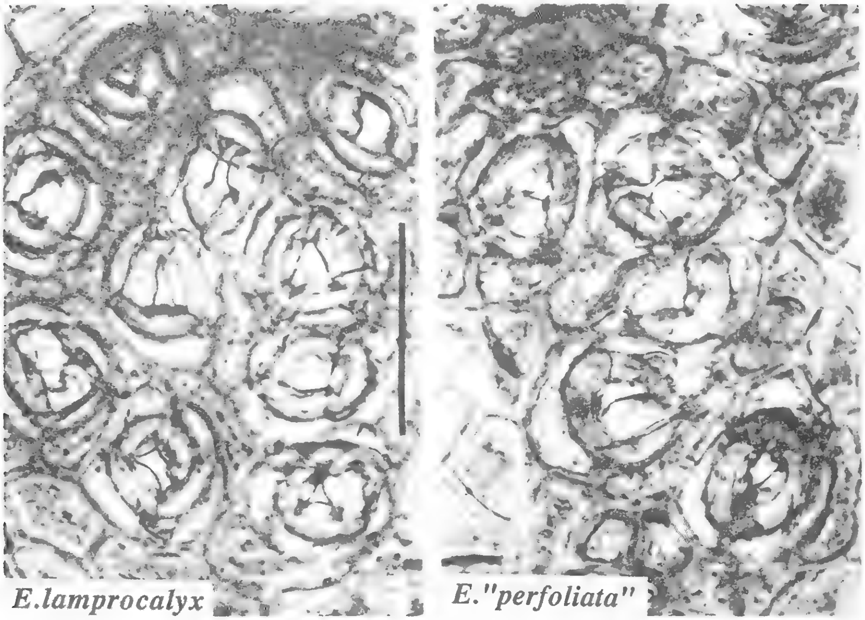


Fig. 20. E. lamprocalyx (isotype) and *E. 'perfoliata'.* Identical phytoglyphs supporting identity of specimens. Scale bar: 50µm. See also legend to Fig. 16.

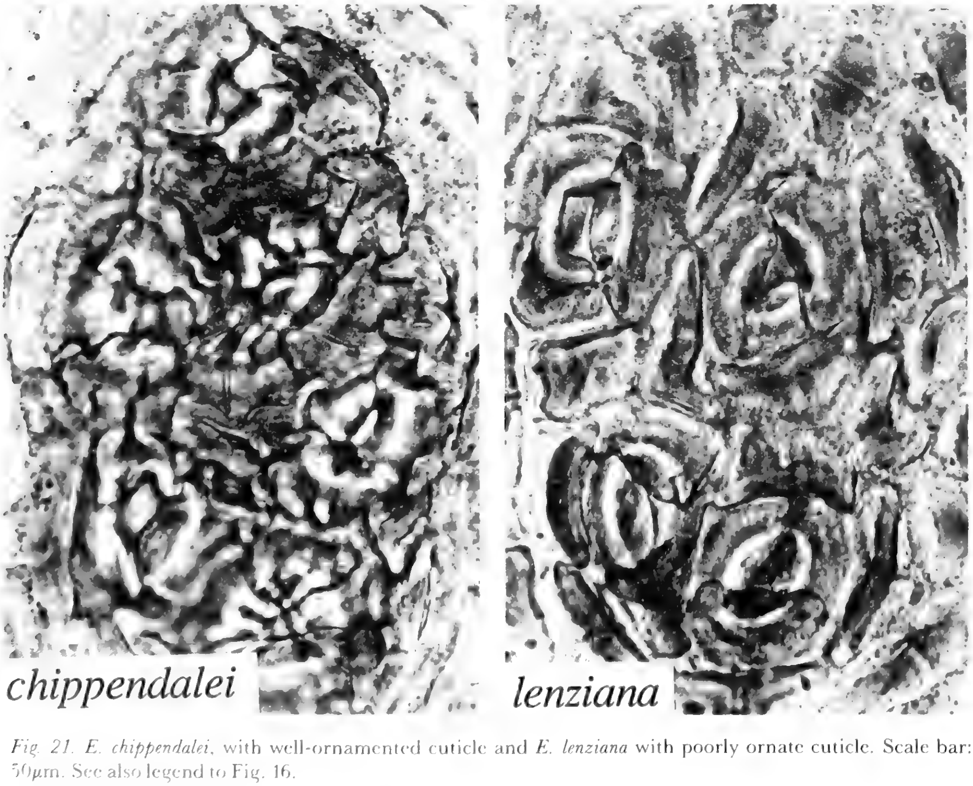


Fig. 21. E. chippendalei, with well-ornamented cuticle and *E. lenziana* with poorly ornate cuticle. Scale bar: 50µm. See also legend to Fig. 16.

On the other hand, the cuticular ornamentation of closely related species, such as *E. lenziana* and *E. chippendalei*, may be quite different in appearance (Fig. 21). These differences may therefore be of very great diagnostic value, especially when the two species (the relationship between which may be evident, as they are in this case, from similarities of a number of macroscopic features) occur together in the same region.

These examples are intended to show how phytoglyphic features, taken together with comparisons of the macroscopic features of leaf, fruit and flower can be used to establish identity between specimens of the same species or, alternatively to establish that they are of different species. Since Mueller's time, many publications have appeared testifying to the usefulness of such microscopic features of the leaves in taxonomy. Since palaeobotanists often have only fossilized leaves to work with, they have pursued the study of such features much more intensively than taxonomists of living plants. Unfortunately, all too few Australian botanists, other than one or two palaeobotanists, have paid any attention to these features of either living plants or fossil leaves. For both Monocotyledons and Dicotyledons it is now, however, *the general consensus that the pattern and shape of the leaf epidermal cells and features of their cuticles are species-specific and differ from one taxon to another* (Barthlott and Ehler, 1977).

Cell patterns involve the distribution of different types of epidermal cells and their positional relationships to each other and to the underlying tissues (e.g. of the veins) (Barlow and Carr, 1984). The presence and the distribution of idioblasts other than stomata (e.g. the cap cells of oil glands, emergent oil glands, hairs etc.) in the epidermis affects these patterns in species-specific ways. For instance, the first-formed stomata of the leaf are so-called 'giant stomata'. They arise near the margin and near the midrib, positions on the leaf primordia which remain fixed, relatively to the rest of the lamina, since marginal meristem activity in eucalypt leaf primordia ceases very early in development. Later on, some more giant stomata may be laid down in the intervening and expanding region of the lamina. In this region, the giant stomata may occupy positions near the centre of vein islets or over the junctions of smaller veins. These are also sites at which epidermal cells may differentiate to form the initials of oil glands. Oil gland initials may also arise early in leaf development near the margin and near the midrib. Thus in both situations, there is some interchangeability between the initials of oil glands and giant stomata, idioblasts which therefore compete, as it were, for preferred positions in the epidermis. On the other hand, neither oil glands nor giant stomata are a constant feature of the pattern and some species (e.g. *E. opaca*) exhibit a dearth of both in their leaf cuticles.

We have already referred to 'giant stomata' as actinocytic, i.e. they generally have a halo of numerous subsidiary cells so that they differ in appearance from the ordinary stomata. Such giant stomata were reported to be a feature of a number of Myrtaceae by Bandulska (1923; 1928-31), who found them on fossilized leaves of Myrtaceae in the Eocene of the London Clay deposits. Solereder (1908) who also reported the existence of giant stomata in some mangrove species referred to them as 'water stomata'. This is a misnomer. There is no evidence as far as we are aware, of a function of these stomata in secreting water. Nevertheless, some recent writers, including Stace (1965) have persisted in using the term 'water stomata'. Van Cotthem (1971) refers to them as hydathodes (in e.g. *Buxus* spp.). Van Wyck *et al.* (1982) also refer to 'water stomata' of the leaves of South African species of *Eugenia*. Napp-Zinn (1973-74) doubts the existence of giant stomata and declares his astonishment that Sitholey and Panda (1971) report on the giant stomata of *Mangifera indica* and *Limonia acidissima*, without giving measurements of their actual size. Indeed, in terms of the length of the guard cells, the so-called giant stomata may, in some cases, not be larger than the ordinary stomata. Solereder reported 'water stomata' as either larger than or smaller than, the ordinary stomata. Nevertheless,

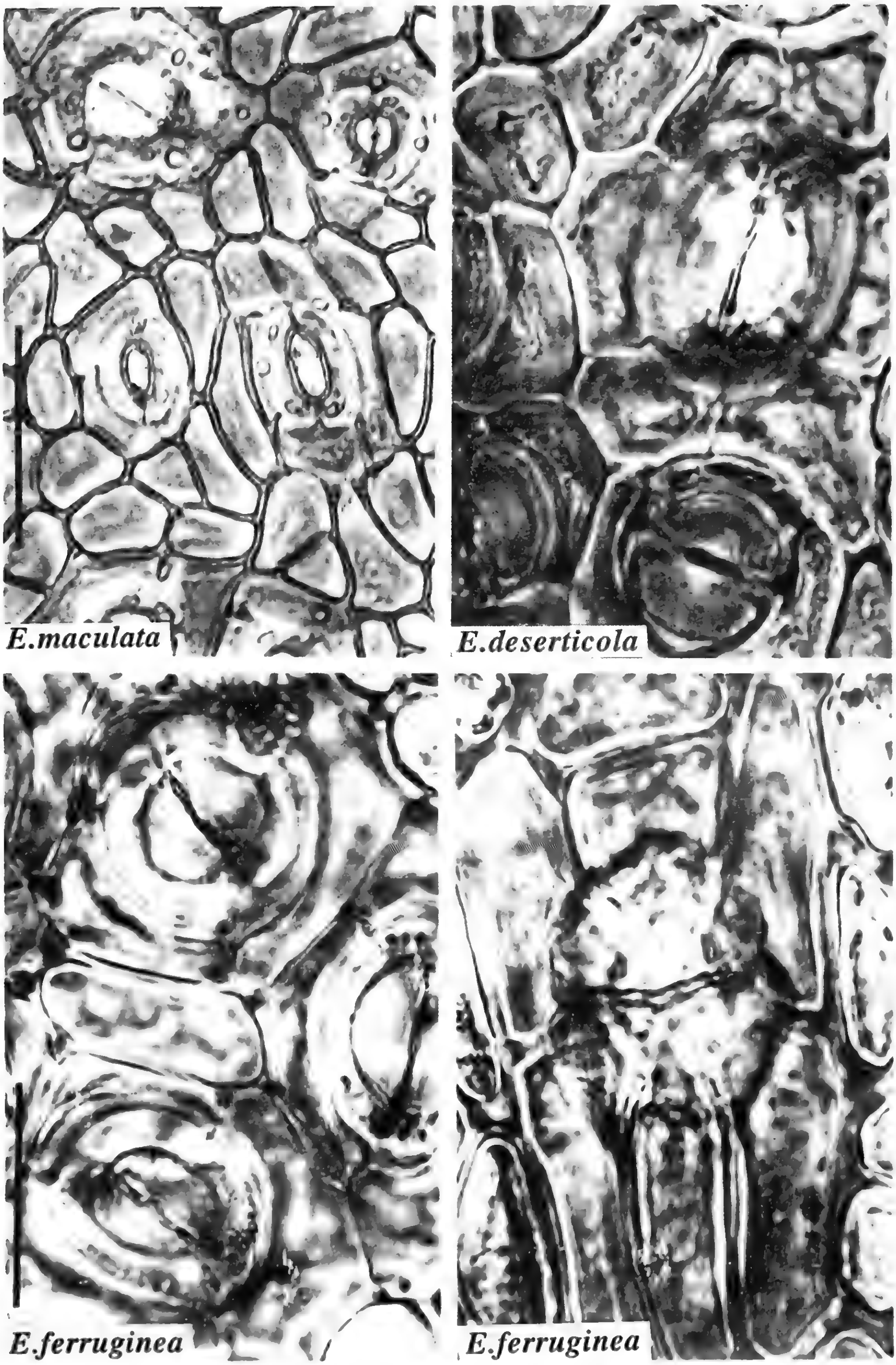


Fig. 22. Giant stomata of *E. maculata*, *E. deserticola* and *E. ferruginea*, in comparison with ordinary stomata of these species. Scale bar: 50μm. See also legend to Fig. 16.

because of their larger complement of subsidiary cells, the giant stomata do stand out as different from — and their guard cells are indeed in most cases larger than — the ordinary stomata (Fig. 22). This is the case in many of the species of the *Corymbosae.* In addition, the cuticular ornamentation of the subsidiary cells of giant stomata is often less ornate or well-developed than that of the subsidiary cells of ordinary stomata.

Quantitative aspects of phytoglyphic features of the *Corymbosae*

We have already touched on two quantitative aspects of the phytoglyphic features of the leaves, *viz*, differences in stomatal size between two species and the possibility of a very low stomatal density of the upper surface of the leaves in some species. Between related 'heterogenous' species (to use Mueller's term) the density (number per unit area) of the stomata on the upper surface may be quite different. *E. derbyensis*, for instance has up to 90 stomata per square mm, as compared to the 1 per square mm in the related *E. polycarpa.*

Frequency-spectra of the subsidiary cells

The difference between giant and ordinary stomata in the number of subsidiary cells is not the only such difference. Even among the ordinary stomata some will have 3, some 4, some 5, etc. subsidiary cells. If one makes counts of the subsidiary cell complement of a hundred stomata the percentage of 3s, 4s or 5s, etc. appears to be a reproducible characteristic of the species. For instance even a glance at a cuticle of a specimen of *E. centralis* shows that most of its stomata have 3 subsidiary cells (Fig. 23), whereas in a

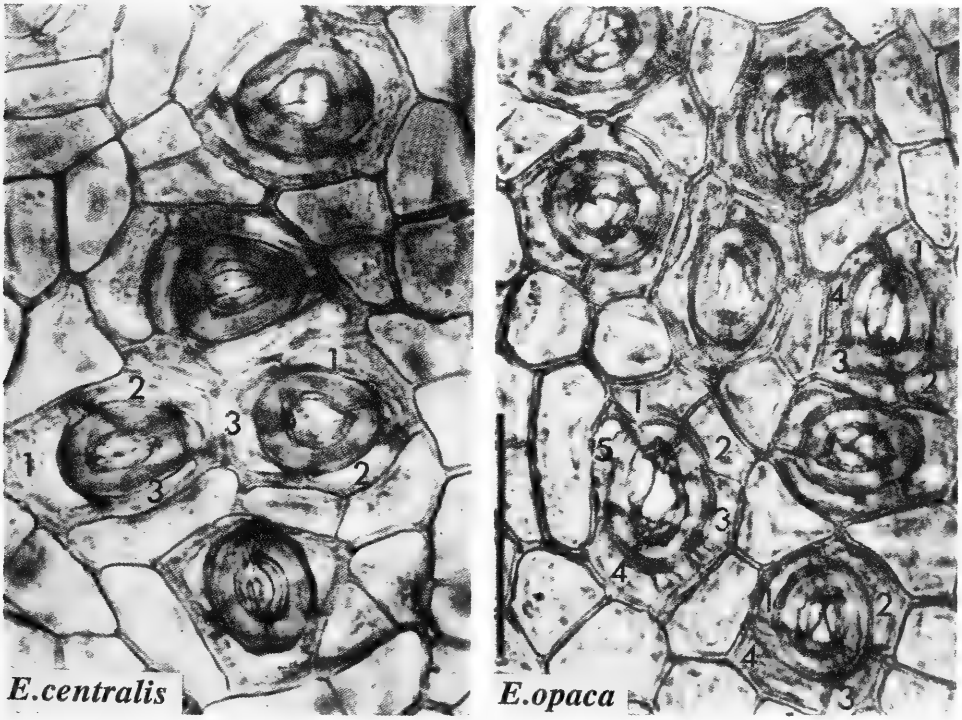


Fig. 23. E. centralis. All stomata in field each with 3 subsidiary cells, to compare with *E. opaca*, some stomata with 4, some with 5 subsidiary cells. Scale bar: 50μm. See also legend to Fig. 16.

similar cuticle preparation of the related *E. opaca*, there are more usually 4 or 5 subsidiary cells to each stoma. Before we consider the exciting possibilities of the diagnostic uses of such *frequency-spectra* of subsidiary cells we must first enquire into their constancy or otherwise in a single leaf, in different leaves of a single specimen, and between different specimens of a single species. Taking the latter first, we see (Table 1) that between 5 specimens of *E. centralis* there are no differences between percentage of 3s to a very high level of probability. The very much smaller percentages of 4s and 5s would require very large samples to be taken (perhaps 500 or 1000) to show whether or not the percentages are repeatable from specimen to specimen. The figures shown are based on counts numbering between 100 and 200. Another feature is shown by the table: the upper surface generally has a lower percentage of 3s than the lower. The percentages of both 3s and 4s on the upper surface is the same in all the specimens, to a very high degree of probability. The frequency-spectra of 6 specimens of *E. centralis* are shown in the graphs (Fig. 24). Evidently the spectra are highly reproducible from one specimen of a given species to another.

TABLE 1

Eucalyptus centralis

5 different specimens

	lower				upper			
Subsidiary cells (%)	3	4	5	6	3	4	5	6
Specimen								
Ford 50	90	7	1	0	83	17	0	0
Carr 752 (type)	89	11	0	0	84.5	15	0.5	0
Jacobs 143	90	11	0	0	80	16	4	0
George 12954	84	15	1	0	84	15	1	0
Frith 49	86	12	2	0	79	18	3	0
Means	87.8	11.2	0.8	0	82.1	16.4	1.7	0
χ^2	0.066	2.929	—		0.312	0.427	—	
	$P>0.95<0.98$		n.s. $(P<0.90)$		$P>0.99$		$P=0.98$	

The method of sampling to obtain the data was, using an oil-immersion objective and a stained, *inverted* cuticle preparation, to count the subsidiary cells of two or three stomata in a microscope field, then move to another field, repeating the process until over 100 counts had been obtained. By subsidiary cells, we mean all the cells which have a wall or part of a wall in common with one or both of the guard cells (see below, for a discussion of this definition). If possible, the preparations for this purpose were taken from the middle third of the leaf. Will any leaf from a given specimen suffice for this procedure? To test this, preparations were make from 5 leaves of a single specimen and counted. The data (Table 2) show that the 5 leaves yield frequency-spectra which are, to a very high degree of probability, identical. Again, the same sorts of differences between upper and lower surfaces are apparent, as in Table 1. There is a tendency for the spectra of the upper surface to be shifted along the abscissa, as compared with the lower. But this is not universally the case, as experience has shown us.

If the middle portion of a leaf is not available, will it make a difference if we use some other part? To test this a single leaf was cut into 5 transverse strips, tip to base. Evidently (Table 3) there is no statistical difference, to a high degree of probability, between the tip, the middle and the base. But a word of caution is necessary. Both tip and base are narrower than the middle and in them the margin and midrib come closer

TABLE 2

Eucalyptus orientalis Carr 763 (type)
5 different leaves

	lower				upper			
Subsidiary cells (%)	3	4	5	6	3	4	5	6
Leaf 1	60.4	31.6	6.4	1.6	47.5	44.17	6.6	1.6
Leaf 2	57.89	32.46	7.29	1.7	49.19	42.74	8.1	0
Leaf 3	58.6	32.3	6.77	2.25	48.62	40.37	10.1	0.9
Leaf 4	57.6	35.2	6.4	0.8	48.8	47.4	3.15	0.78
Leaf 5	58.18	36.36	6.4	0	49.8	44.53	4.45	1.2
Means	58.53	33.178	7.74	—	48.78	43.84	6.47	—
χ^2	0.0865	0.49127	1.5247		0.0588	0.065	4.75559	
	$P>0.99$	$P>0.95$	$P>0.90<0.95$		$P>0.99$	$P>0.95<0.98$		n.s

TABLE 3

Eucalyptus ollaris
5 zones, tip to base, of a single leaf of Carr 827

	lower				upper			
Subsidiary cells (%)	3	4	5	6	3	4	5	6
Zone 1 (tip)	72	25.4	2.6		62.7	28.4	8.8	0
Zone 2	72.75	24.62	2.625	0	62.2	35.43	2.36	
Zone 3	73	24	3	0	64.6	27.4	7.96	0
Zone 4	70.37	26.85	2.77	0	63.41	31.45	3.23	1.6
Zone 5 (base)	72.41	25.82	1.76	0	61.19	30.59	8.2	0
Means	72.17	25.338	3.88	—	62.88	30.65	6.11	—
χ^2	0.01825	0.19054	—		0.11129	1.9305	—	
	$P>0.9$	$P>0.99$			$P>0.99$	n.s. ($P<0.90$)		

together. These latter are regions in which there are concentrations of giant stomata, which, with their unusually large number of subsidiary cells, could affect the comparisons we wish to make. In addition, there might be 'edge-effects' on the frequencies of subsidiary cells even in ordinary stomata in the vicinity of the margin and midrib. These effects could be quite disturbing in especially narrow leaves (e.g. those of *E. nelsonii* and *E. fordeana*). To test for these edge effects we made use of leaves of *E. opaca*, which as we have already mentioned, have relatively few giant stomata. The stomata were sampled close to the margin and close to the midrib and the data compared with counts made half-way between those regions (Table 4). Evidently there is an appreciable edge-effect, especially on the upper surface, where the percentage of 3s is only two-thirds that of the stomata of the intervening region. The recommendation is, therefore, to avoid counting close to the margin and midrib.

Use of the frequency-spectra in the *Corymbosae*

We have made great use of this quantitative aspect of the phytoglyph. It is particularly useful in distinguishing between specimens of two species from the same general area. For instance, *E. centralis* (with a preponderance of 3s) is readily distinguishable (Fig. 24) from *E. opaca* (Fig. 25), which occurs together with it in the same regions of central Australia and the Great Sandy Desert. The specimens used for these graphs

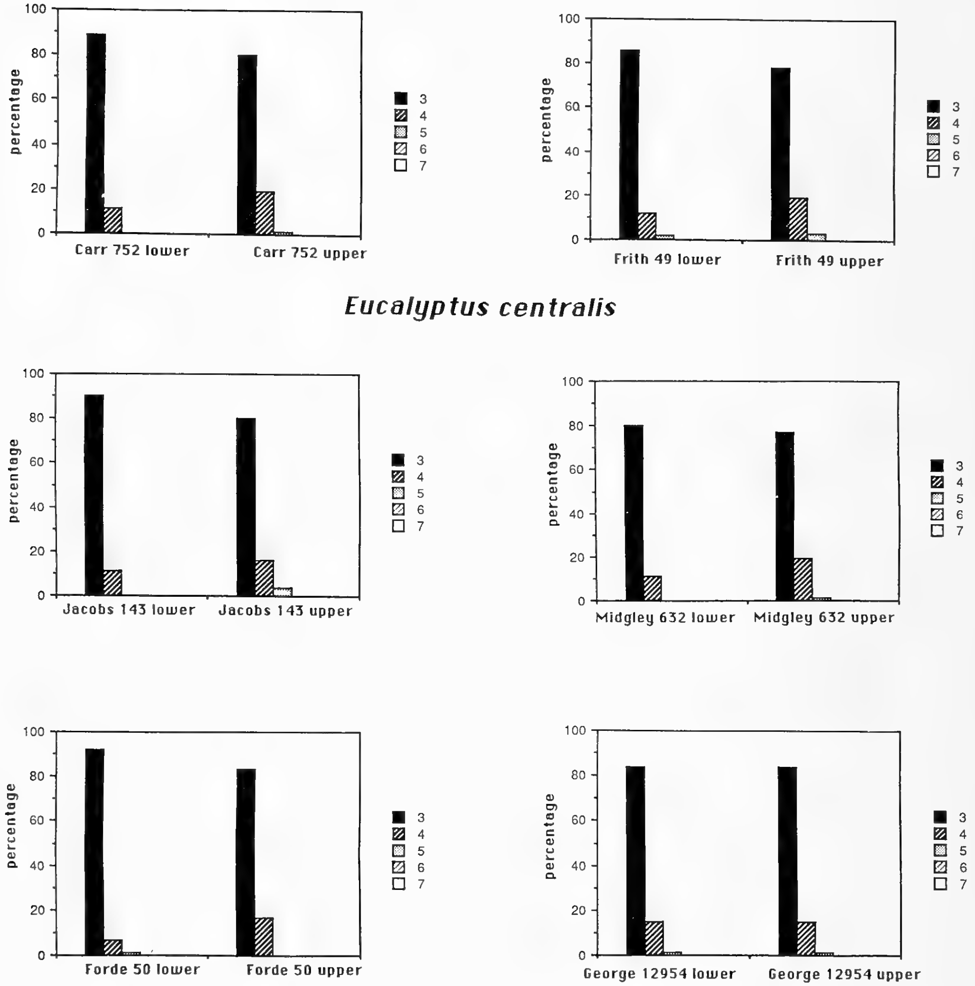
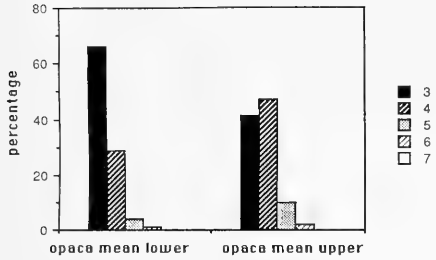
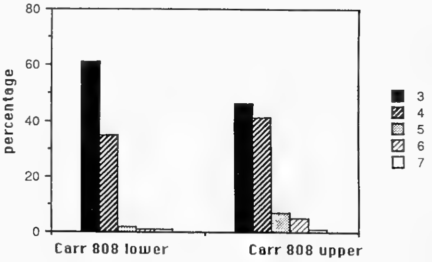


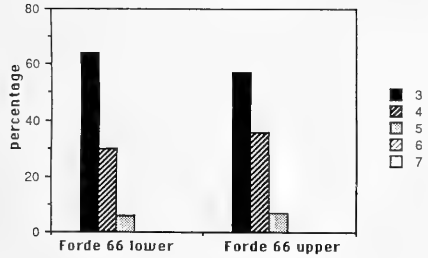
Fig. 24 and *Fig. 25* (opposite). Frequency spectra of *E. centralis* and *E. opaca*. Each separate graph represents a single specimen or the means of several specimens. On the left of each graph, the frequency-spectrum (f-s) of the lower surface, on the right the f-s of the upper surface.

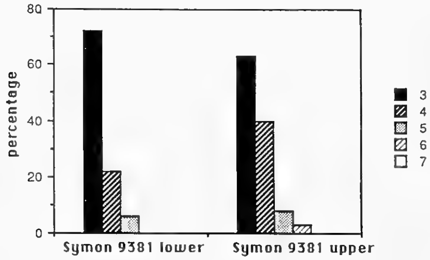
were drawn from widely separated regions, in the Northern Territory and in Western Australia. Specimens of three other central Australian species, *E. eremaea*, and the mountain top mallees, *E. nelsonii* and *E. fordeana*, are also readily distinguishable by their frequency-spectra (Fig. 26). The Forrest specimen of *E. fordeana* was collected in 1883 by the explorer, John Forrest, on the summit of Mt Augusta in Western Australia, a locality very distant from the localities in central Australia from which the other specimen was obtained. Nevertheless, the frequency spectra match. The frequency spectra of widely disjunct specimens of three other central Australian species, *E. symonii*, *E. australis* and *E. connerensis* (Fig. 27) are also consistent and enable the specimens to be grouped unequivocally.

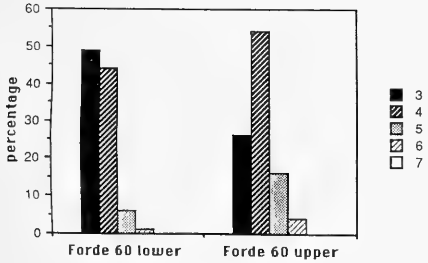




Eucalyptus opaca







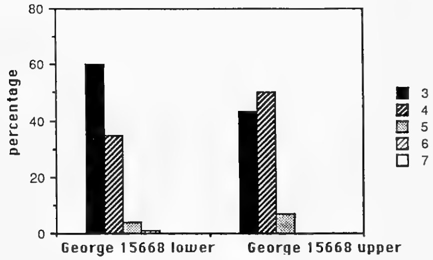
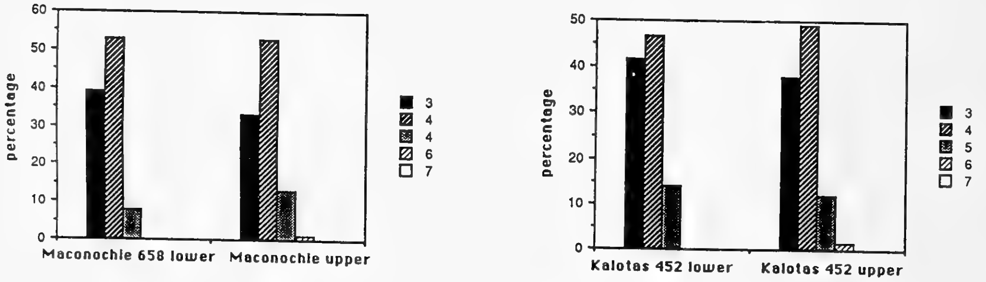


TABLE 4

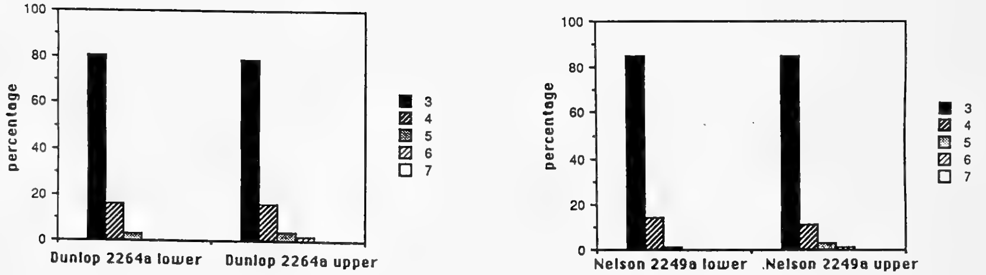
Eucalyptus opaca Carr 808

Edge effects: counts near the midrib, near the margin and in intermediate regions of the leaf lamina

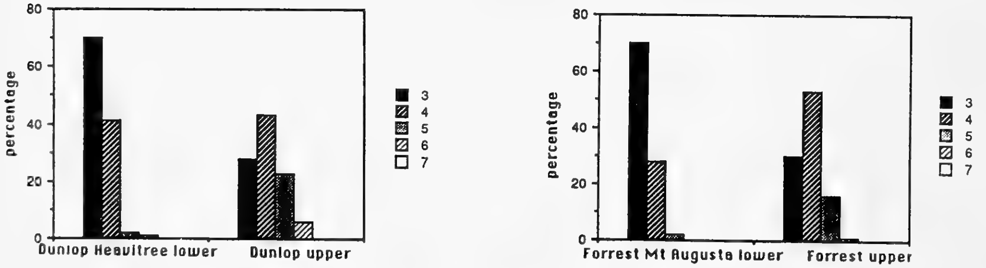
	lower					upper			
Subsidiary cells (%)	3	4	5	6	7	3	4	5	6
intermediate	68.57	27.6	2.86	0.95	0	62.39	34.19	3.4	0
near midrib	62.7	34.9	1.58	0.79	0	39.27	48.2	9.82	2.68
near margin	57.27	36.36	4.545	0.9	0.9	38.68	54.72	6.6	0
Means	62.85	32.95	2.995	0.9	—	46.78	45.70	6.6	—
χ^2	0.038	0.8687	0.006	—		5.2089	2.8989	—	
	P>0.95	<0.98	n.s. P<0.90	P>0.99		n.s. (P<0.05)	n.s. (P<0.05)		



Eucalyptus eremaea



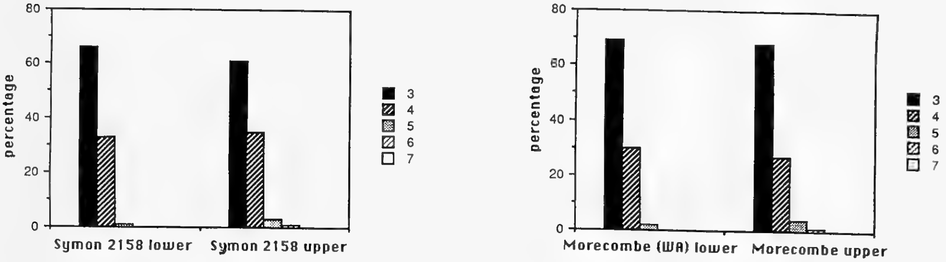
Eucalyptus nelsonii



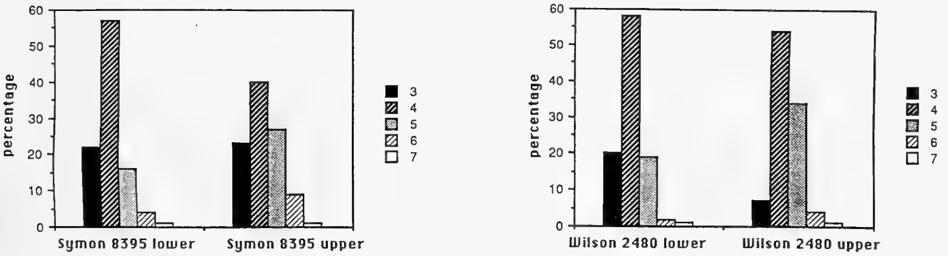
Eucalyptus fordeana

Fig. 26. Frequency spectra of *E. eremaea*, *E. nelsonii* and *E. fordeana.*

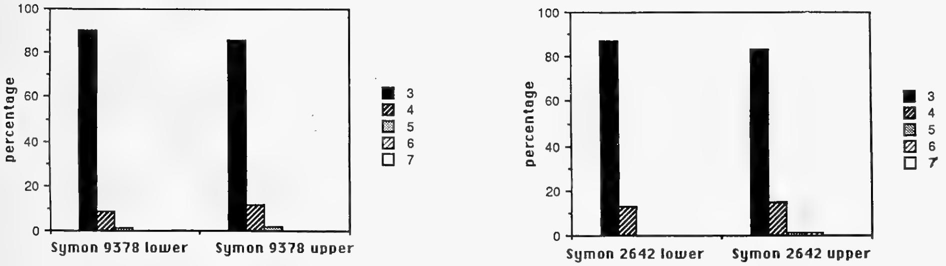
In northwestern Western Australia, specimens of two species with somewhat overlapping distributions, *E. pyrophora* and *E. bynoeana* are also readily separable by their frequency-spectra (Fig. 28). Again, in Queensland, specimens of two species, *E. pocillum* and *E. capricornia*, which occur together in a number of areas have quite different frequency spectra (Fig. 29). It is also to be noted that a Northern Territory specimen of *E. capricornia* (Lazarides 7094) has the same frequency spectra as the Queensland



Eucalyptus symonii



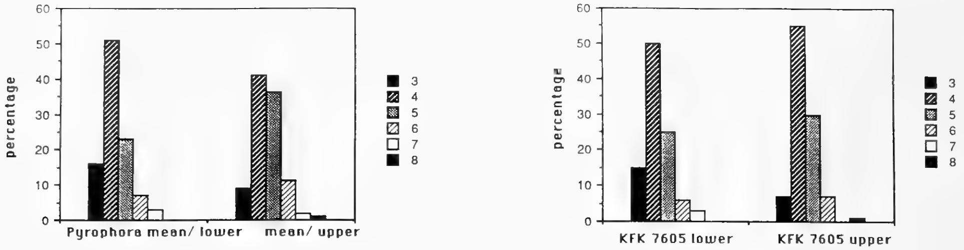
Eucalyptus australis



Eucalyptus connerensis

Fig. 27. Frequency spectra of *E. symonii*, *E. australis* and *E. connerensis*.

specimens. This again confirms that, in general, the frequency spectra of widely disjunct specimens of a given species match each other. These quantitative aspects of the phytoglyph are thus of great help in grouping widely disjunct specimens of the same species as well as in discriminating between pairs of sympatric species. The frequency-spectra thus constitute an invaluable tool in dealing with species of the *Corymbosae*. Its potential value in dealing with other groups of eucalypts has still not been assessed, but we recently made some preliminary observations which showed that seedlings of *E. paliformis* and *E. fraxinoides* (*Renantherae*) have useful quantitative phytoglyphic differences.



Eucalyptus pyrophora

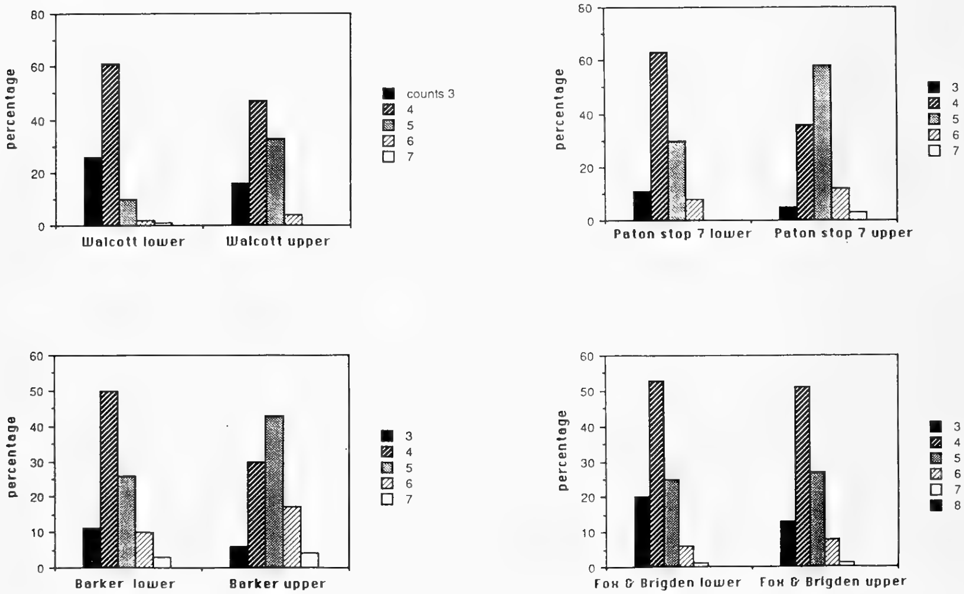
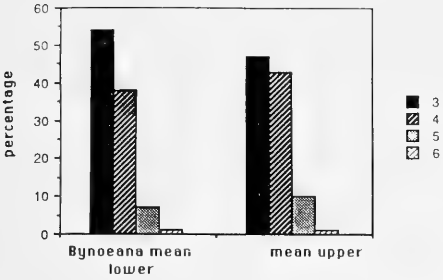
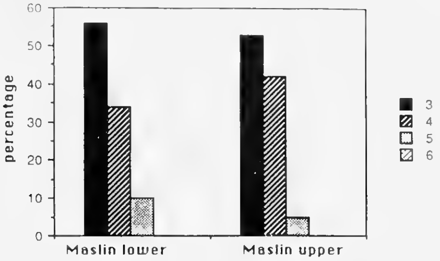


Fig. 28. Frequency spectra of (**1**) *E. pyrophora*, (**2**) *E. bynoeana.*

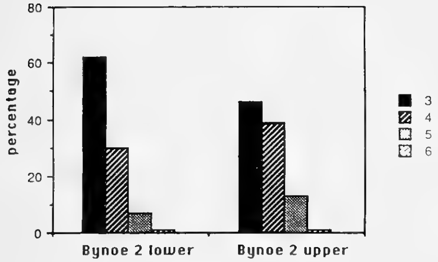
Consideration of frequency-spectra in terms of development

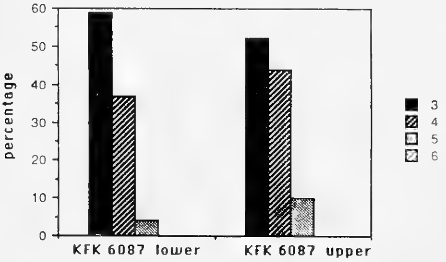
The basal number of subsidiary cells in the anisocytic stomata of the *Corymbosae* is three. We may consider that higher numbers arise from segmentation of the original 3 subsidiaries in the stomatal complex (Fig. 30). There are two possibilities for division of these initial cells. If each divides once, radially, the stoma will have 6 subsidiary cells; if only one, or only two, divide radially the number will be 4 or 5. Alternatively, one or more subsidiary cells may divide radially more than once, to give 7, 8 or 9 subsidiary cells. This is evidently more likely to occur during the development of giant stomata. The second possibility is that the proto-subsidiary cells divide, not radially, but peripherally. This would leave the subsidiary cell complement at its original number, *if we consider the subsidiary cells as those which have a portion of cell-wall in common with one or both of the guard cells.* In the Commelinaceae, for instance, the stoma may be surrounded by a series of rings of cells, forming a rosette which develops by successive peripheral divisions of 2 or 4 subsidiary cell initials (Tomlinson, 1969). We would use the term subsidiary cells for the innermost cells, those which actually share a wall with the guard cells. In connection with such cases, Napp-Zinn (1973) discusses the problem of

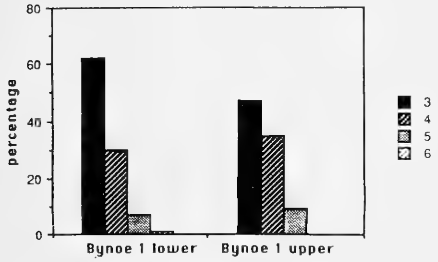


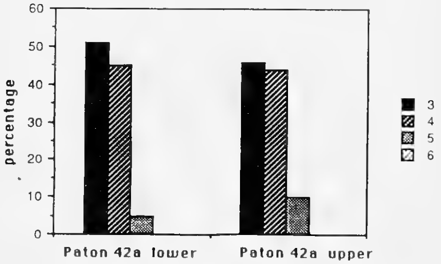


Eucalyptus bynoeana

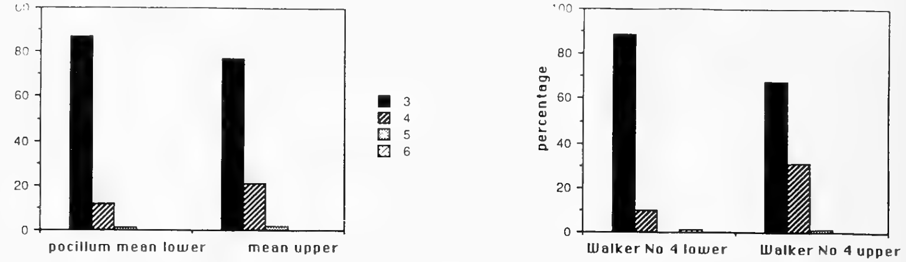








definition of the term 'subsidiary cell', pointing out that many authors use the term not only for the innermost cells, as defined above, but also for what he terms 'encircling cells' (*Kranzzelle*) which may or may not owe their developmental origin to the single stomatal initial from which the rest of the stomatal complex is derived. Korn's studies of stomata were directed, not to the numbers of subsidiary cells, but to the spacing and pattern of distribution of stomata in the epidermis. Discussing the helicocytic (sequentially spiral) divisions of the stomatal initials of *Sedum stahlii* (Crassulacaeae), the last division of which produces the guard cells, surrounded by (in our definition) 3 or 4 subsidiary cells but, according to Korn, 6 subsidiary cells, Korn (1972) states that: 'Regardless of which cells are true subsidiary cells, the methods employed in models discussed here used cell distances from a developmental aspect and not from the final position of cells. It can be suggested here that perhaps subsidiary cells of *Sedum stahlii* are not subsidiary cells in the traditional sense but may serve as spacers to give ordered arrangements of stomata'. Whether or not the outer rings of cells in cyclocytic stomata, such as those of some genera of Combretaceae (Stace, 1963) and Myrtaceae (Bandulska, 1928-1931) have a



Eucalyptus pocillum

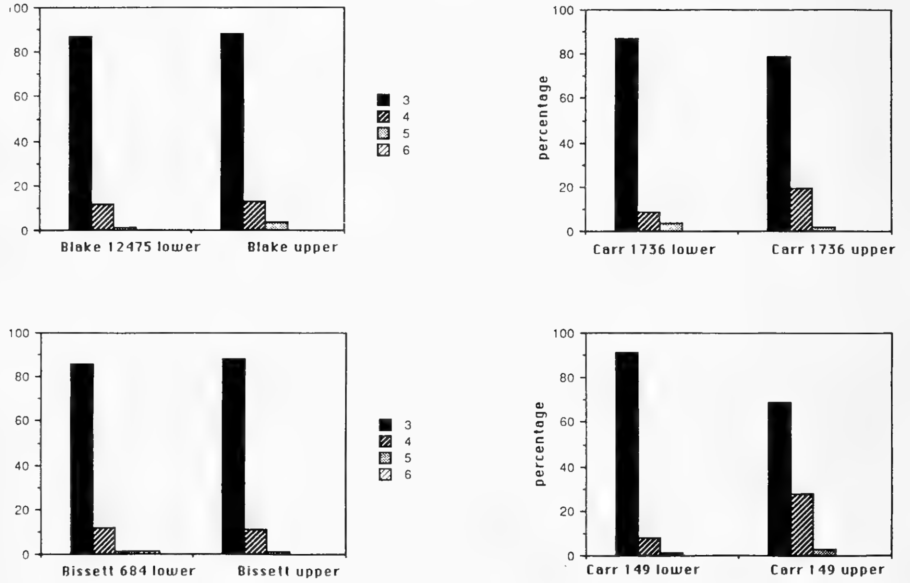
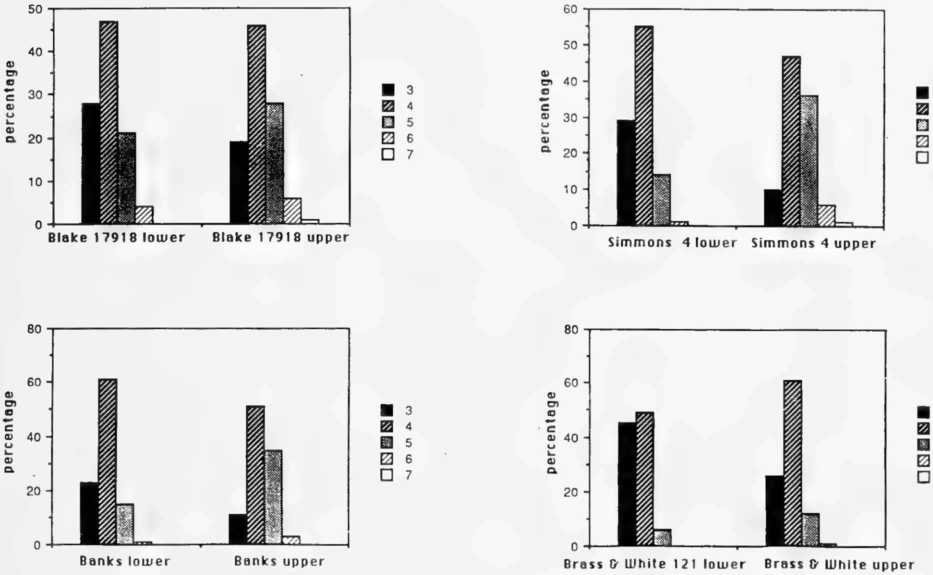


Fig. 29. Frequency spectra of (**1**) *E. pocillum*, (**2**) *E. capricornia*. Lazarides 7094 is a specimen of the latter from Northern Territory; the others are from Queensland.

physiological function in stomatal opening and closing like that of the innermost cells is, of course, unknown.

Evidently the species-specific frequency-spectra of the *Corymbosae* must be genetically determined. This must also be the case for the rather rigid, almost mechanical sequences of divisions in many genera of Monocotyledons. It must be true also of families and genera of Dicotyledons in which the patterns of cell division of the stomatal complexes lead to specific and recognized 'types' of stomata, in which the numbers and arrangement of subsidiary cells, either 2, 3 or 4, are fixed and relatively invariant. Some of these patterns have been recognized as characteristic of whole families of flowering plants, e.g. the 'cruciferous', 'ranunculaceous' and 'rubiaceous' types. Because of their recurrence in many families, not only those after which they were named, these types are now classified more objectively in terms of the number and arrangement of the subsidiary cells in the stomatal complexes. A considerable number of 'stomatal types' have been recognized (van Cotthem, 1970; Fryns-Claessens and van Cotthem, 1973; Dilcher, 1974; Wilkinson, 1979). Such classifications have led to the recognition of the widespread distribution of particular 'stomatal types'. For instance, the Magnoliales,

Eucalyptus capricornia



sensu Takhtajan, have a nearly uniform occurrence of paracytic (i.e. 'rubiaceous') stomata, held by some writers to be a primitive type. In the Piperaceae, for instance, the stomata have been described as helicocytic and cyclocytic (van Cotthem, 1971). These relatively 'standard' patterns and numbers must be the products of sets of developmental steps, themselves the resultants of genetic programming by a relatively invariant segment of the genome which is widely distributed in the species and genera of a number of families. This genetic programme determines the pattern and number of divisions giving rise to the stomatal complexes and therefore determines the number of subsidiary cells. Evidently the execution of the developmental steps involved may be subject to occasional aberration but, by and large, the genetically-determined end product will be predominant.

In the *Corymbosae*, the genetic control of the frequency-spectra must also operate by determining the number and orientation of the cell divisions in the cell complexes of the stomatal initials, which are basically anisocytic. We may speculate that the cells, other than guard cells, of the complex have an initial capacity for cell division which is, within certain limits, determined genetically so that there is a statistical probability of a certain mean number of cell divisions, with less probability of fewer or more divisions. Moreover, the general orientation of these cell divisions, either predominantly radial, as in *E. zygophylla* and the related *E. deserticola*, or predominantly peripheral, as in

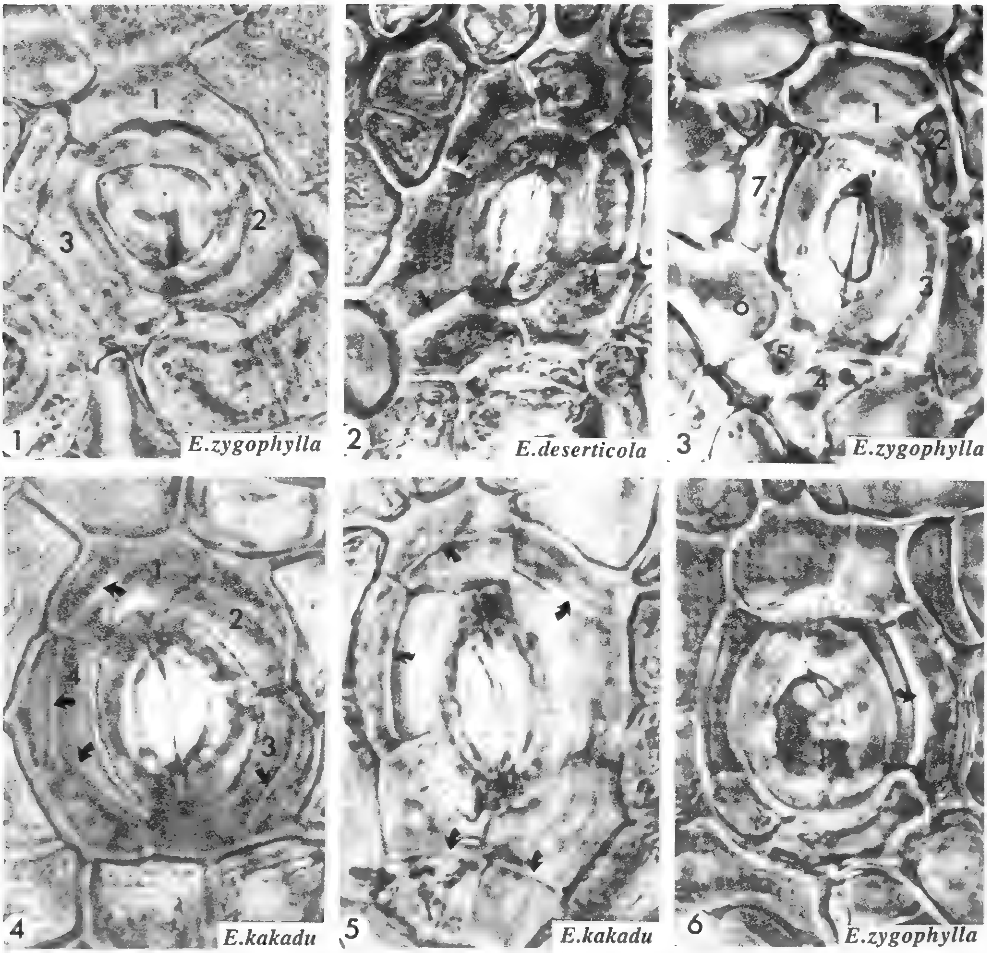


Fig. 30. Stomata to show radial subdivisions (**1-3**) and peripheral subdivision (**4-6**) of the initial subsidiary cells. All to the same scale. Scale bar: 50μm.

E. kakadu, must also be subject to genetic control. One interesting corollary of this view is that there must be genetic determinants which result in the patterns of distribution and of cell division in the stomatal complexes being, in general, different on the lower and the upper surfaces of the leaf.

The differences between Monocotyledons, with their almost mechanical, *deterministically-controlled* patterns of cell divisions in the stomatal complexes and the Dicotyledons, many families and genera of which appear at first glance to have patterns of cell-division which are much more *statistically-determined*, is paralleled by the developmentally-determined orientation of the guard cells in the Monocotyledons and the somewhat random arrangements in many (but not all) Dicotyledons.

References

BANDULSKA, H., 1923. — A preliminary paper on the cuticular structure of certain Dicotyledonous and Coniferous leaves from the Middle Eocene of Bournemouth. *J. Linn. Soc. Lond. Bot.* 46: 241-269.

——, 1928/31. — On the cuticles of some recent and fossil Myrtaceae. *J. Linn. Soc. Lond. Bot.* 48: 657-671.

BARLOW, P. W., and CARR, D. J., (eds), 1984. — *Positional Controls in Plant Development.* Cambridge: Cambridge University Press.

BARTHLOTT, W., and EHLER, N., 1977. — Raster Elektronenmikroskopie der Epidermis-Oberflächen von Spermatophyten. *Tropische und Subtropische Pflanzenwelt.* 19, Mainz.Akad.Wiss.u.d.Literatur. Wiesbaden: Steiner.

BLAKE, S. T., 1953. — Botanical contributions of the Northern Australia Survey. I. Studies on Northern Australian species of *Eucalyptus. Aust. J. Bot.* 1: 185-352.

CARR, D. J., and CARR, S. G. M., 1978. — Origin and development of stomatal microanatomy in two species of *Eucalyptus. Protoplasma* 96: 127-148.

——, and ——, 1980a. — *Eucalyptus* stomata with occluded anterior chambers. *Protoplasma* 104: 239-251.

——, and ——, 1980c. — The *Lehmannianae:* a natural group of Western Australian eucalypts. *Aust. J. Bot.* 31: 629-643.

——, and ——, 1985. — *Eucalyptus I. New or little-known species of the Corymbosae.* Canberra: Phytoglyph Press.

——, and ——, 1987. — *Eucalyptus II. The rubber cuticle and other studies of the Corymbosae.* Canberra: Phytoglyph Press.

CARR, S. G. M., 1972. — Problems of the geography of the tropical eucalypts. *In* D. WALKER, (ed.), *Bridge and Barrier; the natural and cultural history of Torres Strait*: 153-181. Canberra: A.N.U., Dept Biogeogr. and Geomorph. Publ. BG/3.

——, and CARR, D. J., 1976. — Identification of a eucalypt fragment, based on anatomy of leaf and stem. *Proc. Roy. Soc. Vict.* 88: 77-82.

——, and ——, 1979. — An unusual feature of stomatal anatomy in certain taxonomically-related *Eucalyptus* spp. *Ann. Bot.* 44: 230-243.

——, MILKOVITS, L., and CARR, D. J., 1971. — Eucalypt phytoglyphs: the microanatomical feature of the epidermis in relation to taxonomy. *Aust. J. Bot.* 19: 173-190.

CUTLER, D. F., ALVIN, K. L., and PRICE, C E., (eds), 1982. — *The Plant Cuticle.* Linn. Soc. London, Symp. No. 10. London: Academic Press.

DILCHER, D., 1974. — Approaches to the identification of angiosperm leaf remains. *Bot. Rev.* 40: 1-157.

FRYNS-CLAESSENS, E., and VAN COTTHEM, W., 1973. — A new classification of the ontogenetic types of stomata. *Bot. Rev.* 39: 71-138.

KORN, R. W., 1972. — Arrangement of stomata on the leaves of *Pelargonium zonale* and *Sedum stahlii. Ann. Bot.* 36: 325-333.

MAIDEN, J. H., 1909-1928. — A critical Revision of the Genus Eucalyptus. Vols I-VIII. Sydney: Government Printer.

MARTIN, H. A., and JUNIPER, B. E., 1970. — *The Cuticles of Plants.* London: Edward Arnold Ltd.

METCALFE, C. R., 1983. — Secretory structures: Cells, cavities and canals. *In* C. R. METCALFE and L. CHALK, (eds), *Anatomy of the Dicotyledons.* 2nd edition, II: 64-69. Oxford: Clarendon Press.

MUELLER, F. VON, 1874. — *Observations on new vegetable Fossils of the auriferous Drifts.* 2nd decade. Geological Survey of Victoria. Melbourne: Government Printer.

——, 1879-1884. — *Eucalyptographia, a descriptive Atlas of the Eucalypts of Australia etc.* Melbourne: Government Printer.

NAPP-ZINN, K., 1973. — Anatomie des Blattes. II. Angiospermen, A.I. *Encyclopaedia of Plant Anatomy*, viii (2A). Berlin, Stuttgart: Gebrüder Borntraeger.

NEVILLE, A. C., 1963. — Daily growth layers in locust rubber-like cuticle influenced by an external rhythm. *J. Ins. Physiol.* 9: 177-186.

SITHOLEY, R. V., and PANDEY, Y. N., 1971. — Giant stomata. *Ann. Bot.* 35: 641-642.

SMITH, H. G., 1908. — On the elastic substance occurring in the shoots and young leaves of *Eucalyptus corymbosa* and some species of *Angophora. J. Proc. Roy. Soc. N.S.W.* 42: 133-146.

SOLEREDER, H., 1908. — *Systematic Anatomy of the Dicotyledons.* Transl. L. A. BOODLE and F. E. FRITSCH: revised D. H. SCOTT. Oxford: Clarendon Press.

STACE, C. A., 1965. — Cuticular patterns as an aid to plant taxonomy. *Bull. Brit. Mus. (N.H.) Bot.* 4: 1-78.

TOMLINSON, P. B., 1969. — *Anatomy of the Monocotyledons.* III. *Commelinales-Zingiberales.* Oxford: Clarendon Press.

VAN COTTHEM, W. R. J., 1970. — A classification of stomatal types. *Bot. J. Linn. Soc. Lond.* 63: 235-246.

——, 1971. — Vergleichende morphologische Studien über Stomata und eine neue Klassifikation ihrer Typen. *Ber. dtsch bot. Ges.* 84: 141-168.

VAN WYCK, A. E., ROBBERTSE, P. J., and KOK, P. D. F., 1982. — The genus *Eugenia* (Myrtaceae) in southern Africa: the structure and taxonomic value of stomata. *Bot. J. Linn. Soc. Lond.* 84: 411-56.

WELCH, M. B., 1923. — The secretory epidermal cells of certain eucalypts and angophoras. *J. Proc. Roy. Soc. N.S.W.* 57: 218-228.

WILKINSON, H. P., 1979. — The plant surface (mainly leaf). Part I Stomata. *In* C. R. METCALFE and L. CHALK, (eds), *Anatomy of the Dicotyledons.* 2nd edition, I: 97-117. Oxford: Clarendon Press.

ADDENDUM

After delivery of the lecture, the president of the Society, Dr Peter Martin, kindly supplied us with copies of pages of two books on organic chemistry by Professor John Read F.R.S. in which reference is made to Henry G. Smith's discovery of the rubber cuticles of certain bloodwoods and species of *Angophora*. The works are: *A Textbook of Organic Chemistry. Historical, Structural and Economic*, 3rd ed., London: G. Bell & Sons Ltd, 1948, p. 615, and *A Direct Entry to Organic Chemistry*, London: Methuen & Co. Ltd (Home Study Books), 1948 reprinted 1953, p. 227.

Blue Mountains Ash (*Eucalyptus oreades* R. T. Baker) in the western Blue Mountains

P. GLASBY, P. M. SELKIRK, D. ADAMSON, A. J. DOWNING
and D. R. SELKIRK

GLASBY, P., SELKIRK, P. M., ADAMSON, D., DOWNING, A. J., & SELKIRK, D. R. Blue Mountains Ash (*Eucalyptus oreades* R. T. Baker) in the western Blue Mountains. *Proc. Linn. Soc. N.S.W.* 110 (2), (1987) 1988: 141-158.

Fire is an important factor in controlling the distribution of *Eucalyptus oreades* within its natural range in the western Blue Mountains. The species which is fire sensitive relies on seeding rather than resprouting after fire. In the western Blue Mountains, *E. oreades* produces annual rings in the wood, allowing the age of a tree and dates of fire damage to it to be determined. Stands of *E. oreades* thus allow establishment of a fire chronology in localized areas. In uniform-aged young stands which are undergoing self-thinning the suppressed individuals set seed before the dominant individuals. Trees which survive to become mature are less susceptible to fire damage, developing a bark skirt at the base which protects them from ground-fire damage. The trees enter the high fire risk period of summer with substantial seed reserves stored in capsules in the canopy. Wind-throw is a major cause of death of old trees, already fire- and/or termite-damaged.

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INTRODUCTION

Eucalyptus oreades R. T. Baker, (Blue Mountains Ash), also known as smooth-barked Mountain Ash or White Ash, occurs on plateaus, ridges and in gullies in the Blue Mountains of N.S.W. It is valued locally not only as a beautiful tree but as a species of economic importance. Pole-sized saplings are logged in Newnes State Forest to supply pit props for coal mining. The Explorers' Tree at Katoomba, marked by Blaxland's party when making the first crossing of the Blue Mountains in 1813 is *E. oreades* (Baker, 1919).

The vegetation of the Blue Mountains has been little studied despite the spectacular topography of the region and its proximity to the vast urban area of Sydney. For example, *E. oreades* is not even listed in a recent review of wet sclerophyll eucalypts on the east coast of Australia (Ashton, 1981). Apart from the original description of *E. oreades* (Baker, 1889) and more recent descriptions, with maps, of its Australian distribution (Boland *et al.*, 1984), no botanical publications deal in any detail with the species. Vegetation descriptions of the Mt Wilson area (Brough *et al.*, 1924; Petrie, 1925) include associations which contain *E. oreades* and recognize that aspect and altitude are important factors for its occurrence (Pidgeon, 1938). A vegetation classification of the western region of Sydney (Forster *et al.*, 1977), and the unpublished Forestry Commission 1:25,000 map of Newnes State Forest No. 748, set out its general distribution in the Blue Mountains.

Following studies on the ecology of wet sclerophyll species, particularly *E. regnans*, in Victoria and Tasmania (Ashton, 1958; Gilbert, 1959; Cunningham, 1960; Jackson, 1968), a picture emerged of the interdependence of tall eucalypt forest and fire, a picture which was not generally recognized by early workers on the forests of eastern New South Wales (Brough *et al.*, 1924; Petrie, 1925; Pidgeon, 1937, 1938, 1940; Beadle, 1954, 1962). The response of *E. oreades* to fire is well known in general terms to local staff of the

Forestry Commission and the National Parks and Wildlife Service but no information has been published on its response to fire or on its general biology.

As the urbanized area in the Blue Mountains expands rapidly, particularly along narrow ridges with an intrinsic high fire risk to property, there is increasing demand to minimize that risk by frequent burning, with little knowledge of its effects on the vegetation in general or on certain species in particular. Present-day attempts to manage fire in whole National Parks and in urban bushland areas represent a major change from earlier, more laissez-faire, approaches to fire control, an approach to fire which *E. oreades* survived. With the present trend towards planned intervention in previously unmanaged fire regimes, detailed information on the biology of the plants involved is clearly needed by land managers.

An additional threat to *E. oreades* is the discovery that the Newnes Plateau and adjacent high altitude areas contain huge deposits of sand and clay suitable for deep open-cut mining (Pecover, 1984; Anon., 1984). Implications for the landscape and vegetation of the western Blue Mountains region are severe.

This paper describes aspects of the distribution and life history of *E. oreades* which help to explain its occurrence in the fire-prone landscapes of the western Blue Mountains.

DISTRIBUTION

General

Eucalyptus oreades occurs in a number of disjunct populations within the latitudes 28°15′S to 34°30′S (Fig. 1). The largest population is in the Blue Mountains. Other stands occur on the escarpment inland from Port Macquarie, in the Gibraltar Range between Grafton and Glen Innes, in the Binna-Burra—Springbrook—Mt Warning area near the New South Wales—Queensland border, and near Tenterfield (Boland *et al.*, 1984). The altitudinal range lies between about 700 and 1200 metres. The disjunct distribution could indicate a former, more continuous, distribution.

Blue Mountains

In the Blue Mountains, *E. oreades* occurs on sands and clayey sands derived from Triassic sandstone parent rock in the Katoomba and Grose soil associations (Forster *et al.*, 1977). It also occurs on alluvial and colluvial sands in valleys and deep river gorges, on cliffs, and on sandstone soils whose texture is influenced by deep, red clay loams derived from the basalt caps at Mt Wilson. It would appear that soil depth or type does not explain its distribution in the Blue Mountains.

A striking feature of the species' distribution in the Blue Mountains is its relationship to the spectacular topography. It occurs rarely on exposed ridges but is common on steep sheltered slopes with a southerly aspect and around the heads of valleys facing south and east, on cliffs and cliff ledges, and along creek beds (Fig. 2). In these locations it can occur as individuals, particularly on cliffs, or as dense stands in sheltered valleys (in wet sclerophyll or tall open-forest). On the gentler slopes of the plateaus and ridges extending west from Katoomba to the Newnes Plateau, mature trees develop spreading crowns with short boles and branches low down on the trunk. Such trees have been kept as specimen trees in the towns of the upper Blue Mountains. They also occur as widely spaced individuals in mixed eucalypt open-forest associations (dry sclerophyll). By contrast, trees growing in crowded stands on steep sheltered slopes develop straight tall trunks, topped by a simple domed canopy. These form stands of tall open-forest (wet sclerophyll). Trees growing on ledges and in joints on cliffs develop tall straight, often non-vertical, trunks.

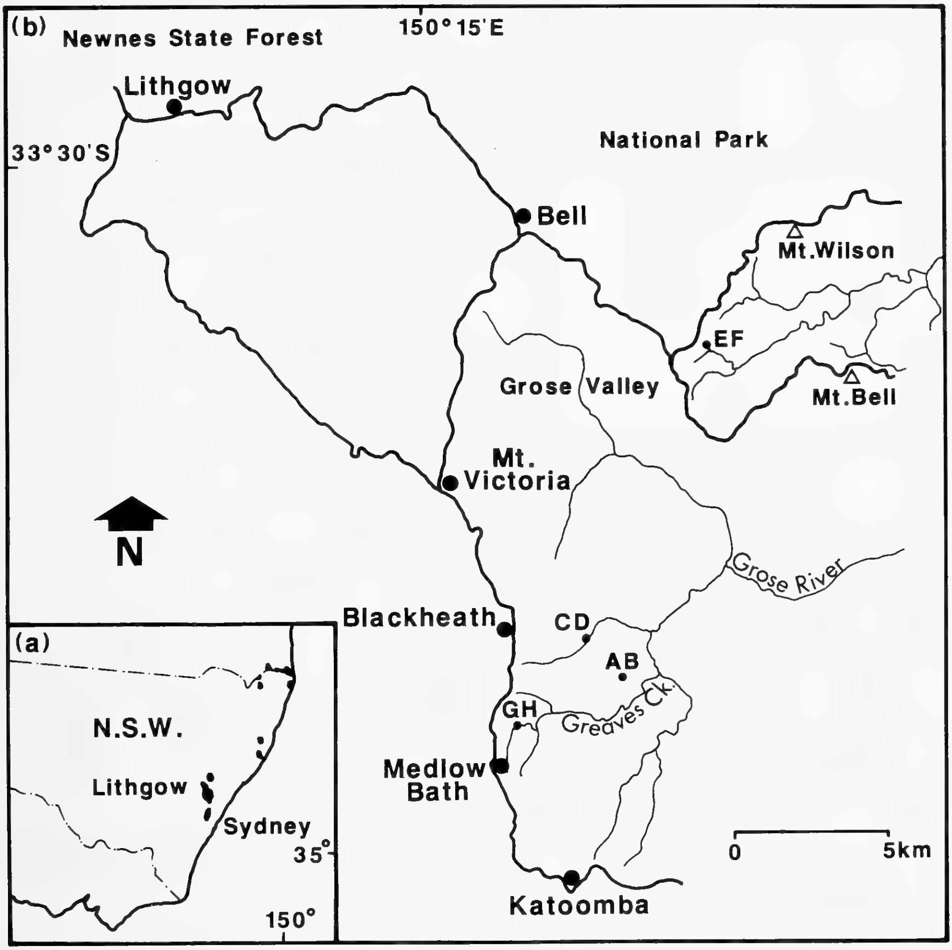

Fig. 1. **a**. General distribution of *E. oreades* (after Boland *et al.*, 1984). **b**. Location of sites in western Blue Mountains mentioned in text. More detailed locations specified in some diagrams.

Measured Transects

Fig. 3 is a downslope section through a tall open-forest of *E. oreades* at Evans Lookout near Blackheath. This site (AB) is typical of dense stands which occur on south-to-east-facing slopes of steep valleys (Fig. 2**b**), particularly near the main drainage lines. The site is below the rim of the plateau and above the first main line of cliffs within a tributary valley of Greaves Creek. An open woodland of eucalypts including *E. piperita* (Peppermint) and *E. sieberi* (Black Ash) grows on the plateau. Closed forest (rainforest) of mainly *Ceratopetalum apetalum* (Coachwood) and *Doryphora sassafras* (Sassafras) occupies the lower parts of the valley below the first main line of cliffs. At this site *Eucalyptus oreades* occupies the typical position of wet sclerophyll tall open-forest: relatively sheltered sites located between the even more sheltered rainforest vegetation below and the more exposed woodland vegetation on ridges and plateaus.

Beneath the *E. oreades* canopy is an open sparse intermediate canopy of *Acacia elata* (Cedar Wattle) and a lower dense canopy dominated by *Callicoma serratifolia* (Black

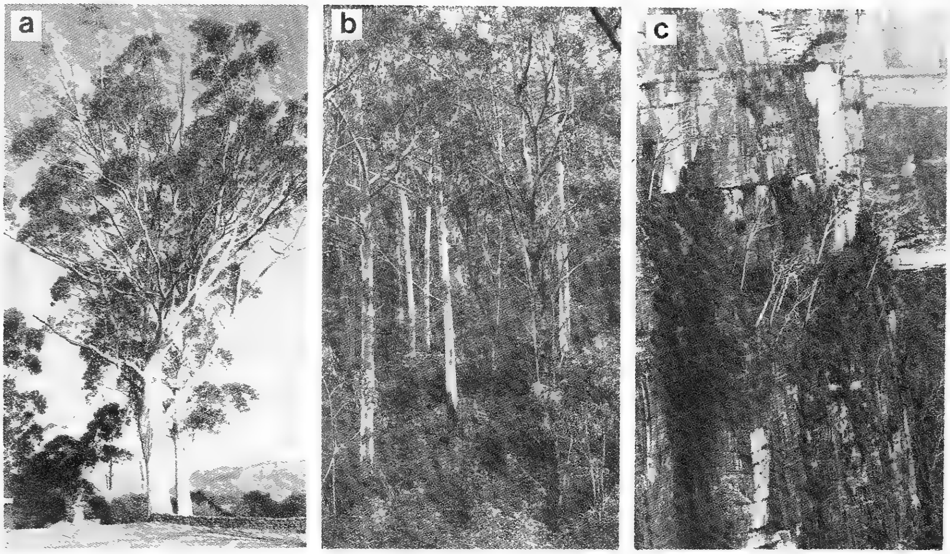

Fig. 2. **a.** Two large spreading *Eucalyptus oreades* trees on an exposed ridge, Gordon Lookout, Leura. **b.** Dense stand of *E. oreades* at the head of a south-facing gully near Evans Lookout, Blackheath (adjacent to transect at site AB, Fig. 3). **c.** *Eucalyptus oreades* trees on cliff face near Govetts Leap, Blackheath.

Fig. 3. Transect at site AB (1981) at Evans Lookout, Blackheath, showing distribution of *E. oreades* at the head of a south-facing valley, between dry sclerophyll woodland on plateau surface and rainforest in lower cliff-bounded valley.

Wattle). Dense clusters of ferns such as *Sticherus lobatus* and litter accumulations ensure very low light levels at soil level.

Fig. 4 presents similar data for two other valley slopes which face between east and south. Site CD is on an east-facing slope of the linear N-S valley of Govetts Leap Brook in an area dominated by woodland, shrubland and heath. Occasional tall trees of Blue Mountains Ash occur near the creek. Site EF, in the upper Bowens Creek Valley, is similar in situation to AB but EF was burnt in a severe fire in December 1979. Severe fire has probably not affected AB since 1959. In each site *E. oreades* clusters on sheltered moist slopes at the head of steep south-facing creeks beneath the scarp of a distinct ridge or plateau.

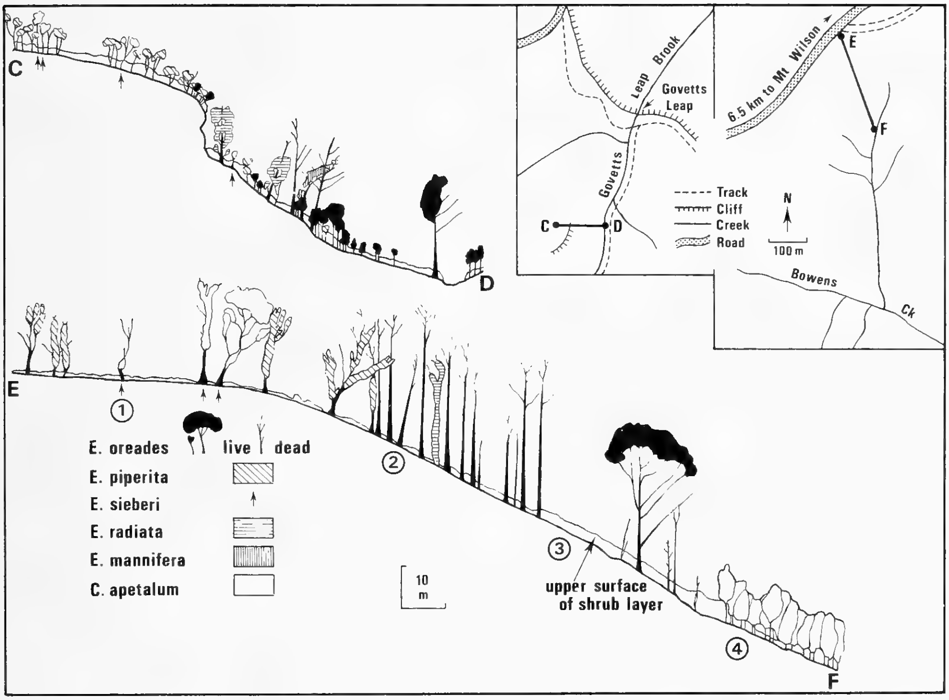

Fig. 4. Transects at sites CD and EF (1981). CD near Govetts Leap, Blackheath, shows live and fire-killed *E. oreades* in a small isolated stand last affected by fire in 1959. The site was again burnt in 1982 (see text). EF is a site where almost all mature trees in a large stand were killed by severe fire in December 1979. Extensive seedling establishment has since occurred.

Site GH (Fig. 5) traverses an asymmetric valley in the headwaters of Greaves Creek between Medlow Bath and Blackheath, where the Blue Mountains plateau is only slightly incised. Again, trees of *E. oreades* cluster on the east-facing steeper slope but widely spaced mature individuals occur in the woodland on the gentle slopes of the plateau. These tall trees project well above the other eucalypts and are usually associated with several small living or dead offspring.

Although the sites in Figs 3 and 4 contain trees of widely different size and age, similar individuals are often clustered. The patchy nature of the stands suggests episodic death and regeneration in response to fire as the causal process.

EFFECT OF FIRE ON STAND STRUCTURE

Baker (1919) noted and we have confirmed that the wood of *E. oreades* grown in the Blue Mountains contained annual rings. Blue Mountains Ash also records fire damage in the wood where the vascular cambium is killed. Using fire scars dated from tree rings, a fire chronology was obtained for the sites AB, CD and EF and the ages of trees of various sizes were determined. Fig. 6**a-c** shows frequency distributions for tree size and the age and fire history of individual trees from these sites based on tree rings. The effect of fire is shown clearly at EF where the severe 1979 fire killed all trees below 0.5m stem diameter and many of those larger. These trees had survived fires in 1975, 1966 and 1959. At EF the survivors after the fire were a few large trees located downhill near the boundary of the closed forest. A swarm of seedlings established in the area occupied by the fire-killed trees and by December 1985 were up to 4m tall and sufficient in numbers to replace the earlier stand despite below average rainfall in 1981-1982 and several months of drought after the fire.

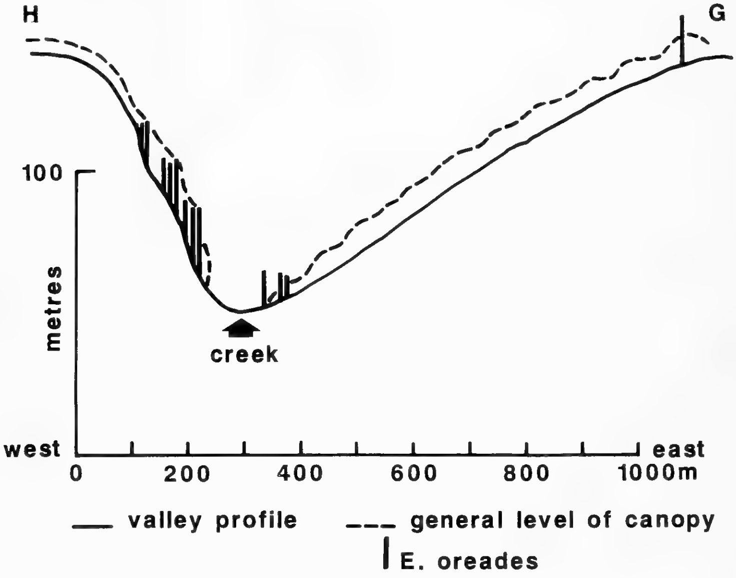

Fig. 5. Transect at site GH (1980), across upper Greaves Creek valley, between Medlow Bath and Blackheath, on the west of and parallel to electricity transmission line.

At Govetts Leap Brook (site CD) the swarm of small trees was killed in a severe fire of late 1982. The one large, mature tree survived but the fire killed half of its canopy and half of its vascular cambium to a height of 1.5m, severely weakening it. Since this fire, only 4 seedlings (up to 0.5m tall in December 1985) have become established.

At the Evans Lookout site (AB) a fire in 1959 was followed by the establishment of a cohort of trees dating from about 1960. This fire burnt patchily in the valley leading to localized death of trees, scarring of others, and the regeneration of new plants. A later less severe fire occurred in 1969.

Each site shows that fire easily kills young trees of *E. oreades* and severe fire, particularly through the canopy, easily kills mature trees. Following each fire there is usually recruitment of a new cohort of plants from seed, leading to the development of a mosaic of even-aged stands of different ages, each stand in its own burn patch. Observation of fire-damaged trees shows that fire kills the live bark and vascular cambium of trunk and branches and that the surviving parts of damaged trees have little capacity to resprout. This sensitivity of individual trees of *E. oreades* is in marked contrast to the vigorous resprouting after severe fire of most other eucalypts in the region.

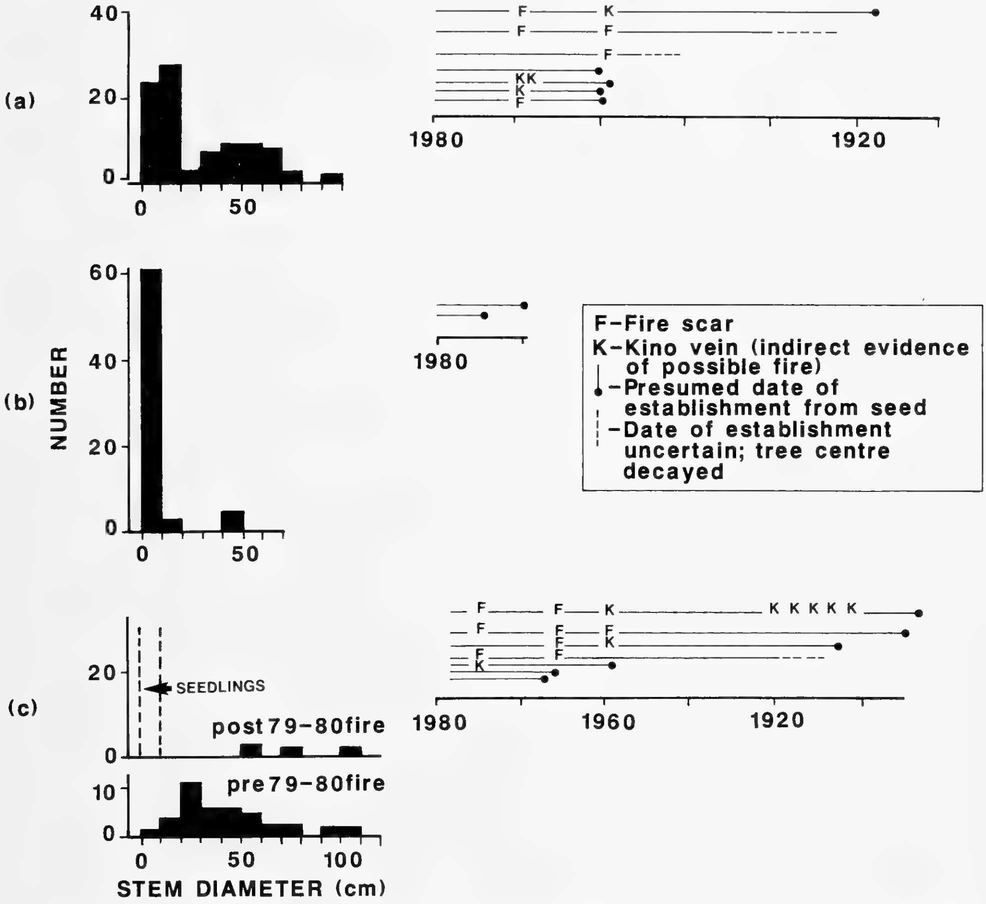

Fig. 6. Frequency distribution in mid-1980 of trees of various diameters with fire history of particular trees inferred from examination of annual rings and fire scars. **a.** Site AB Evans Lookout. **b.** Site CD Govetts Leap Brook. **c.** Site EF Bowens Creek valley.

Establishment of large numbers of plants following a fire leads to strong intra-specific competition and the development of a wide range of size within an even-aged stand. The dominant individuals grow rapidly; the suppressed individuals grow slowly and most die. Fig. 7 shows size classes in such a stand about 12 years after a fire. Trees ranged in height from about 2m to 8m. The most suppressed trees had very little (about 2cm) new growth per shoot, bore capsules from two years, buds and very few leaves. The dominant trees in the stand had extensive new shoot growth (about 30cm per shoot), bore no capsules or buds, and had a crown of dense foliage. After a further four years self-thinning had removed the smallest trees.

TABLE 1

Estimates from counted subsamples of number of buds, capsules, and seed stored in the canopies of three mature wind-felled E. oreades *trees*

	Total per tree						
(age in years)	Buds	Green capsules	Purple capsules	Grey capsules	All capsules	Fully viable seed	Viable seed per capsule
Tree 1 (>100)	24 000	10 000	9 000	2 000	21 000	63 000	3
Tree 2 (> 30)	60 000	36 000	1 000	6 000	43 000	128 000	3
Tree 3 (> 30)	111 000	24 000	4 000	4 000	32 000	96 000	3

SEED PRODUCTION IN SUPPRESSED TREES

A striking feature is that the suppressed trees in the 12-year-old stand produced capsules whereas the dominant trees did not (Fig. 7). Each capsule contained about 3 viable seeds, a similar number to that of mature trees (Table 1). The total number of viable seeds per suppressed plant (average of about 350) was low because of the small number of capsules on each tree although the total number of seeds per unit ground area in the stand was approximately 36,000 per $100m^2$, a substantial fraction (about ⅓ to ½) of that found in a stand of mature trees because of the large number of suppressed plants. The early and effective reproductive behaviour of suppressed trees in a crowded uniform-aged stand constitutes a hedge against a severe fire in the period before the dominant individuals reach maturity. Diversion of resources from vegetative to reproductive growth in the suppressed trees guarantees their early death but provides an early seed bank at that particular site. This behaviour is an effective insurance against a severe fire following between about 10 and 25 years after an earlier one.

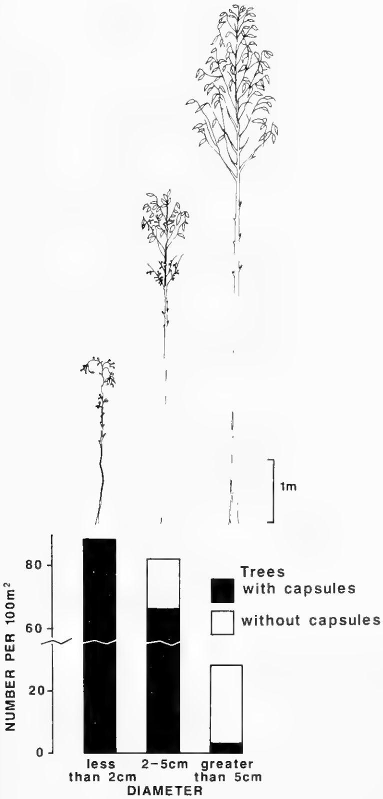

Fig. 7. Size distribution of a dense young stand of *E. oreades* regenerated after clearing and fire in 1969. Drawings are representative of three size classes. Stem diameter measured 10cm above ground level. Stand located at the head of a south-facing valley on the southern edge of the Katoomba Airfield (Medlow Bath).

SEED AND LITTER PRODUCTION IN MATURE TREES

Mature *E. oreades* trees bore three distinct age classes of capsules, as well as developing buds (Table 1). The outermost growing tips of branches bear new vegetative growth and young flower buds which open in summer. Behind these, within the mature leafy area of the branch, are the green capsules from the previous summer's flowering. Further back is an area of small branches usually devoid of leaves which bear purple capsules which are two years old. Still further back on the branches are grey capsules borne either on persistent dead twigs or on the main branch itself. These grey capsules may be three years old or older.

Viability of seeds from the three colours of capsules is shown in Table 2. Only 2% of seeds from green capsules collected in August 1980 were viable, but by October, all ages of capsules contained viable seed. In all capsules larger, heavier seeds were more likely to be viable than smaller, lighter ones (Table 2). *E. oreades* therefore enters the high risk summer fire period with large amounts of viable seed stored in the canopy (Table 1).

TABLE 2

Percentage germination, and weight per seed, of three length classes of seeds from three capsule ages harvested in October 1980 from storm-felled trees

Germination was tested on four replicates of 25 seeds.

The standard errors are given in brackets

Capsule colour	Length of seed (l) longest axis (mm)	% germination	Average seed weight (mg)
green (from Jan 1980 flowering)	$1.8 < l$	89 (±1)	1.9 (±0.02)
	$1.0 < l < 1.8$	59 (±3)	1.5 (±0.03)
	$0.7 < l < 1.0$	3 (±1)	1.0 (±0.02)
purple (from Jan 1979 flowering)	$1.8 < l$	65 (±5)	1.7 (±0.08)
	$1.0 < l < 1.8$	51 (±3)	1.3 (±0.04)
	$0.7 < l < 1.0$	0	0.9
grey (from Jan 1978 or Jan 1977 flowering	$1.8 < l$	45 (±14)	1.3 (±0.15)
	$1.0 < l < 1.8$	25 (±2)	1.0
	$0.7 < l < 1.0$	1	0.8 (±0.02)

Measurements of litter fall (Fig. 8) show the sequence of flowering and capsule development. Flower buds begin development enclosed within two bracts. These bracts are shed mainly in late summer to autumn, although some persist till October. Following bract fall the buds develop further and flowering takes place from mid-January to February. Observations of stands at many sites on the Blue Mountains plateau showed that flowering was synchronous within this period. Flowering occurs as the opercula of the buds fall off (Fig. 8). During flowering and immediately following it, many flowers and immature capsules fall to the forest floor. This is followed by a peak in seed fall during March and April. The seed fall peak precedes the later capsule fall peak, suggesting that seed is released from capsules within the canopy, not from fallen capsules. There is a peak capsule fall in May, the capsules on twigs falling in large numbers. These capsules are mainly purple capsules, although some grey ones fall as well. Each year the grey population is augmented by the purple capsules which escape falling in autumn.

RESPROUTING

The feeble resprouting of burnt *E. oreades* trees contrasts with the vigorous regrowth of other species. Even when the bark and vascular cambium remain alive few epicormic shoots are produced.

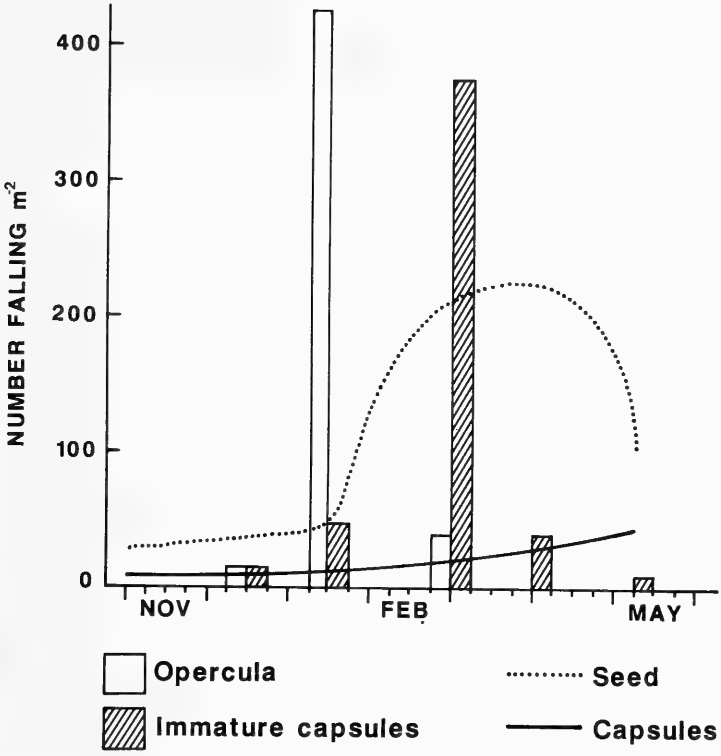

Fig. 8. Seasonal fall of reproductive parts of *E. oreades* in a dense stand (approx. 1000 live trunks of total basal stem area $54m^2$ per hectare). Values are means from 5 traps, each $1m^2$ in area.

A defoliation experiment was conducted to compare the resprouting ability of *E. oreades* with that of two vigorously resprouting species that grow in the same area. *E. piperita* and *E. sieberi* (Fig. 9). *E. oreades* produced significantly less resprouting than the other two species. Additionally, *E. oreades* was slower to produce sprouts than the other two species. Most of the refoliation in *E. piperita* and *E. sieberi* was confined to the top half of the stem while the foliage on *E. oreades* was more uniformly distributed over the whole stem, presumably an inefficient strategy for reestablishment of an upper canopy.

Although the number of resprouts is undoubtedly determined by the number of epicormic buds available, a feature not investigated, the lack of vigour of the shoots may be related to the lower levels of starch in the sapwood of this species in comparison with more vigorous resprouters (Table 3). Photosynthate is apparently devoted to growth in height, girth and canopy development rather than accumulation of starch reserves.

Fire Damage and Decay in Stems

Fig. 10 shows typical fire damage and subsequent recovery in stems of Blue Mountains Ash. Undamaged stems (Fig. 10**a**) show the regular annual increments of wood growth typical of rapid vertical growth where there is a distinct contrast in summer and winter temperatures. Unscarred trunks in mature trees are uncommon. Figs 10**c** and 10**d** show the effect of ground-fire on young saplings. Death of 50% of the circumference of young stems near ground level is common in surviving trees. If heavily damaged trees

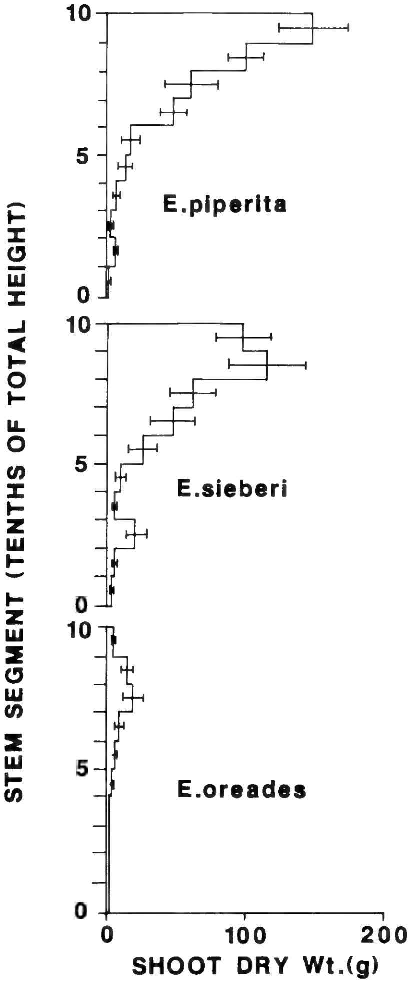

Fig. 9. Dry weight of shoots in each one tenth of stem height (mean of 7 trees) of *E. oreades* measured 143 days after artificial defoliation by pruning on 5 December 1980. Bars are standard errors of means.

TABLE 3

Mean percentage starch in breast height sapwood of three species of eucalypts at Medlow Bath in the Blue Mountains

All trees were about 10 yrs old. The mean is based on samples from six trees of each species taken 14.12.80. An analysis of variance showed a significant difference between the species ($p < 0.01$). Scheffe multiple comparison tests (Pollard, 1977) showed all species were significantly different ($p < 0.01$).

	Mean % Starch (± st. error)	
E. oreades	0.143	(± 0.02)
E. sieberi	0.725	(± 0.15)
E. piperita	1.525	(± 0.26)

survive, the fire scars become sealed within the trunk (Fig. 10**b**). Fire scars provide access for wood-decaying fungi and increase the possibility of fire burning into the centre of the trunk.

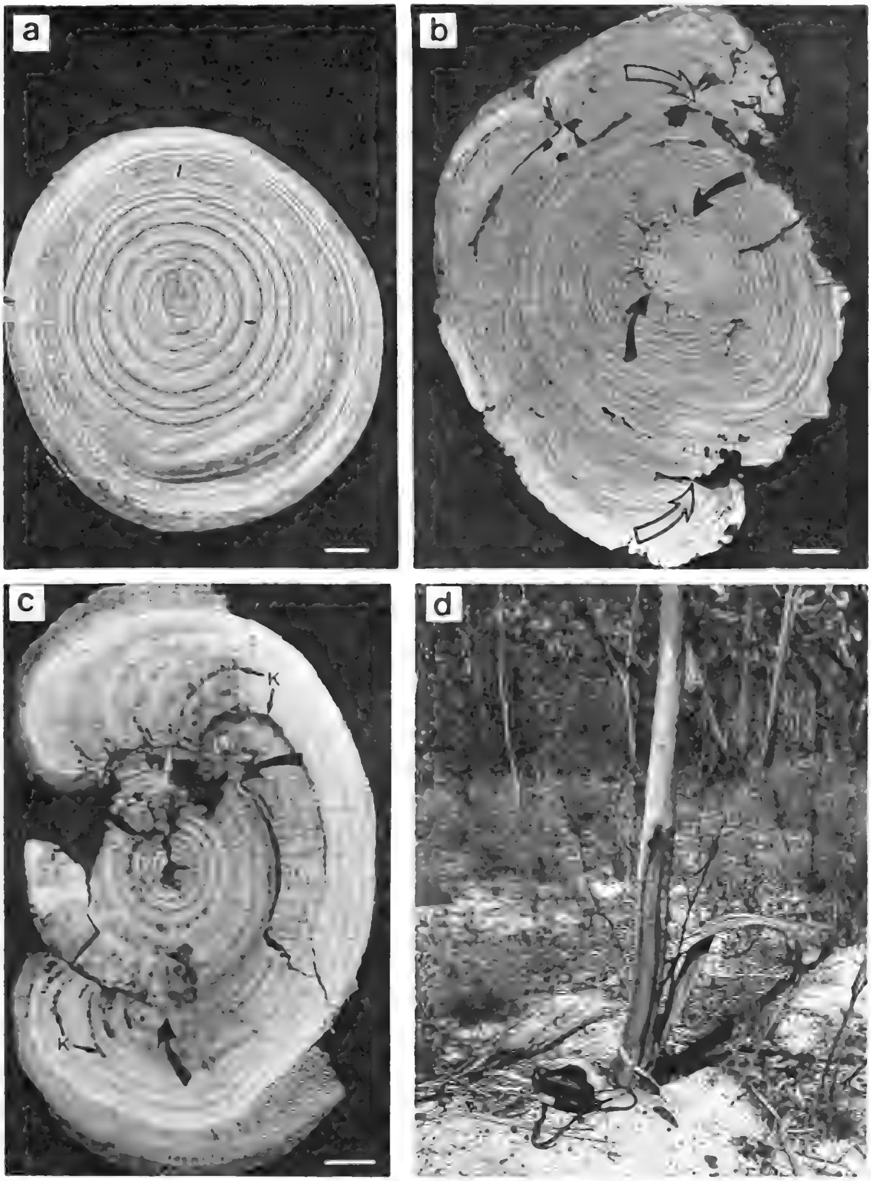

Fig. 10. Eucalyptus oreades. **a**. Cross section of undamaged trunk of tree. Annual growth rings are regular. Scale bar = 1cm. **b**. Cross section of trunk of fire-damaged tree. Cambium was destroyed by fire around ⅓ circumference (between solid arrows) when tree was about 10cm in diameter. This scar has been sealed by subsequent growth. More recently fire has destroyed cambium around nearly half the circumference (between open arrows). Scale bar = 5cm. **c**. Cross section of trunk of fire-damaged sapling. Cambium was destroyed by fire around more than half circumference (between arrows, to left). Subsequent growth has partially covered scar. Note kino veins (K) in wood. Scale bar = 1cm. **d**. Ground-fire has killed about half the circumference of young tree.

As a young tree, *E. oreades* is covered by thin moist live bark, some of which is shed annually. The importance of fire damage to the trunk of *E. oreades* is shown in Fig. 11 where a scheduled winter burn-off caused death to the trees or to sectors of the vascular cambium in trees younger than about 25 years old (15cm stem diameter). Protection from ground fire is provided by a basal skirt of persistent cork which starts to accumulate in trees aged about 20 years and older (Fig. 12). Large trees are afforded a high measure of protection from ground fires by the skirt although it is only effective with ground fires which do not rise high up the trunk. The annual decortication of bark contributes considerably to the fuel accumulation on the forest floor and in the canopy and increases the chance of fires spreading from the ground to the canopy.

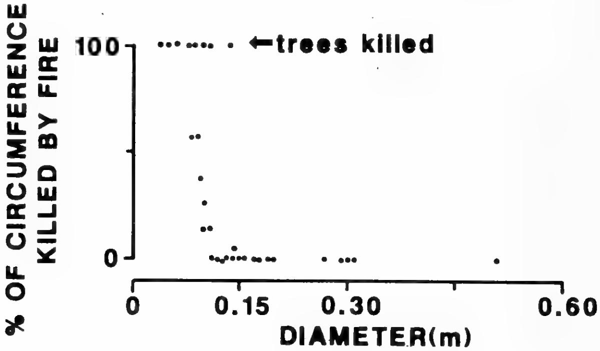

Fig. 11. Cambial death as percent of circumference of *E. oreades* trees at Medlow Bath in a scheduled winter burn in 1978. Measurements taken below 4m above ground level.

Internal decay of the trunks by fungi and termites occurs commonly and possibly in all very large specimens of *E. oreades*. Such decay can be inferred from external scars and fungal fruiting bodies, or directly from the presence of openings or pipes into the heartwood. Baker (1919) noted that the timber was particularly open-textured, that the fibres had delicate walls and large lumens and that the vessels were large and remarkably free from tyloses. Fungi and termites probably gain entry to the heartwood through fire scars such as those illustrated in Fig. 10. Trunks piped by fire are also a common feature (Fig. 13).

WIND DAMAGE

Mature trees usually project well above the level of the surrounding canopy (Fig. 5) and are subject to severe stress from high wind. Strong winds commonly twist and break off the weakened stem well above ground level leaving a standing stump which does not regenerate. Fig. 13 shows a large emergent tree felled by a gale. The thin annulus of sapwood which supported the large canopy was only 4cm thick, the heartwood being completely burnt out.

DISCUSSION

E. oreades is an excellent example of a tree species exhibiting rapid growth and relatively early death (Fig. 14). Dominant trees grow rapidly and achieve heights well above those of most other neighbouring eucalypt species. Suppressed trees grow slowly, become reproductive early and die prematurely but provide insurance against fires spaced about 10 to 25 years apart. Beyond about 25 years the dominant trees develop a seed bank in their canopies and a basal skirt of cork which protects them from groundfires. Up to about this time all trees are extremely vulnerable to fires although the risk

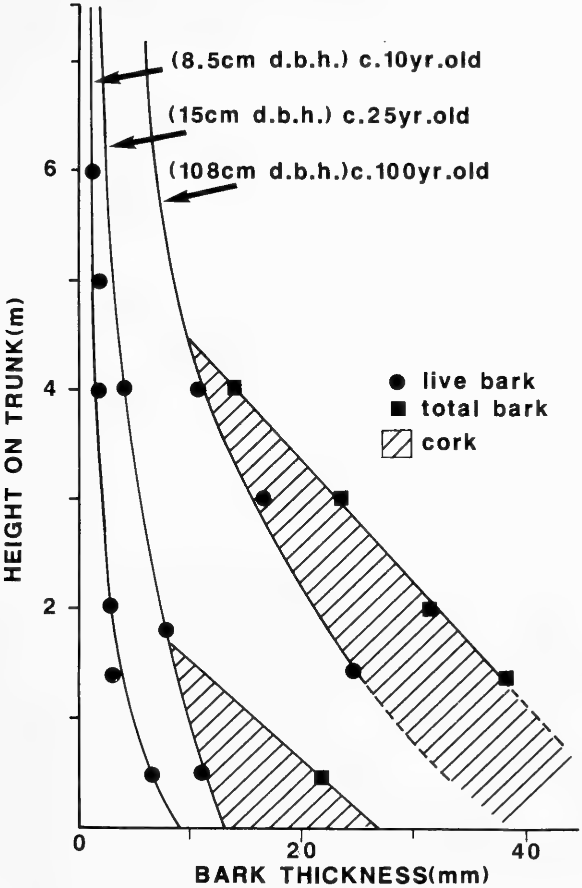

Fig. 12. Relationship between tree height and bark thickness for three *E. oreades* trees. d.b.h. = diameter at breast height. Cork refers to accumulated dead layers of tissue.

from canopy fires declines with tree age as older trees may be tall enough for their canopies to be above the burning zone. Progressive loss of strength in the heartwood makes mature trees that escape death from fire prone to wind collapse, the most likely cause of death of old trees.

E. oreades exhibits reseeding rather than resprouting in response to fire. The damaged plants die and replacement is from seed stored in the canopy. Attributes of the wood and bark, the early seed production of suppressed trees, seed storage in the canopy, rapid growth in height, absence of a lignotuber and sparse epicormic buds are all features appropriate to a reseeding response. Young trees establish from seed stored in the canopy which is shed after fire damage to the parent trees onto an ashbed with abundant light. Early growth of the tree is rapid so that it emerges above regenerating lower storeys of ferns, *Callicoma* and slower-growing trees. Rapid growth in height is an attribute of importance in the densely vegetated and shady south- and east-facing gullies. Regeneration was only observed after fire or other disturbance, such as clearing for transmission lines or landslip, which revealed bare soil and gave access to light. In effect, fire is probably the most important requirement for the establishment of new

Fig. 13. Stump of *E. oreades*, previously hollowed by termites and fire, broken off by wind. Trunk and upper branches on ground to right. Figures give scale.

individuals and stands, but an appropriate fire regime is required for their survival to maturity.

The response to fire by plants of different ages has implications for fire management of areas in which *E. oreades* grows. Complete exclusion of fires will prevent regeneration, shifting the vegetation towards rainforest. The species thrives in areas where occasional severe but patchy fires occur at intervals of several decades (possibly 50 years). Too frequent burning, even by low intensity winter ground fires will kill or excessively scar young trees and eventually prevent regeneration.

ACKNOWLEDGEMENTS

We thank R. Oldfield and J. Norman for preparing photographs, and G. Rankin and B. Thorn for preparing diagrams. The National Parks and Wildlife Service of N.S.W. is thanked for permission to carry out research in the Blue Mountains National Park.

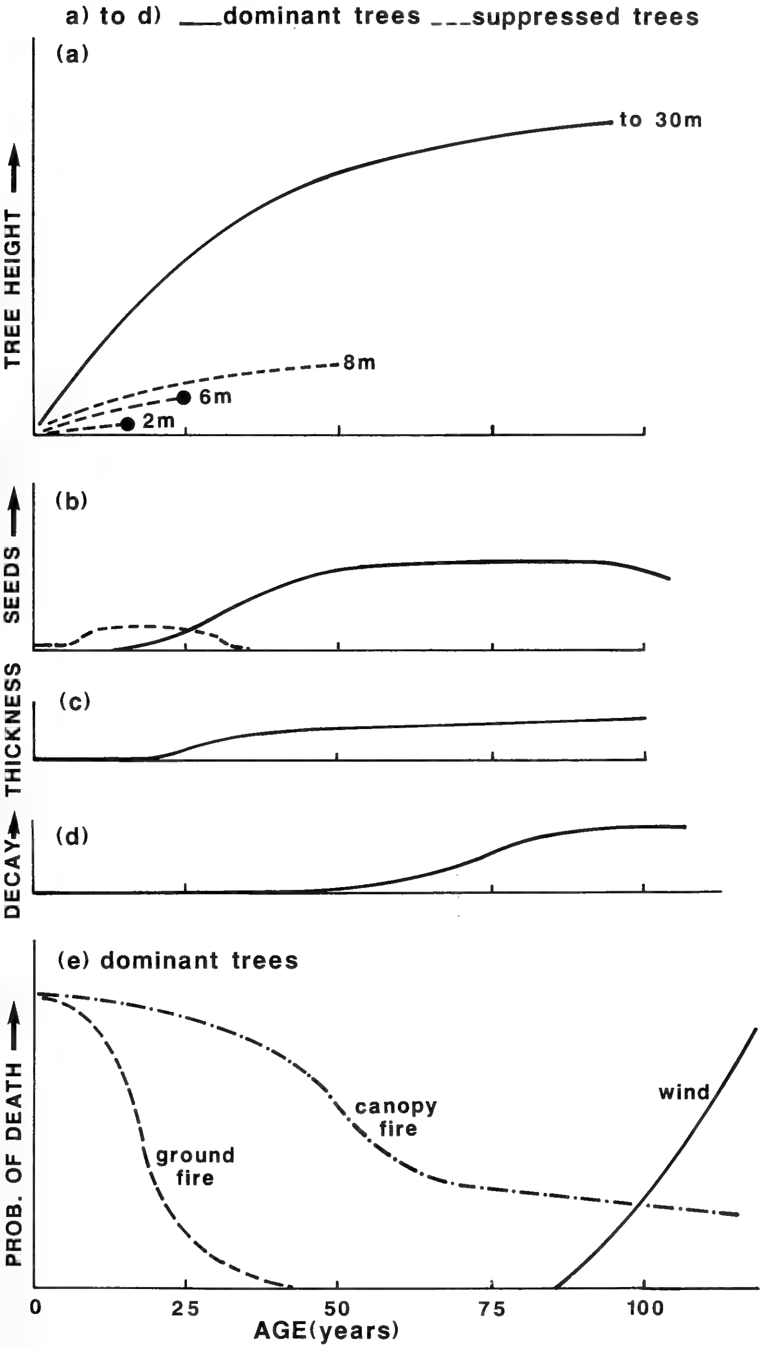

Fig. 14. Notional representation of events in life of *E. oreades* trees in a uniform-aged stand. **a**. Height of dominant and suppressed trees. • death of tree. **b**. Number of seeds per tree on dominant and suppressed trees. **c**. Thickness of cork on lower trunk of dominant trees. **d**. Extent of decay in heartwood of dominant trees. **e**. Probability of death of dominant trees from fire (ground or canopy) or wind throw (after initial piping of stem).

References

ANON., 1984. — Newnes Plateau — a sand resource. *Minfo. New South Wales Mining and Exploration Quarterly.* (Dept Mineral Resources, Sydney): 16-18.

ASHTON, D. H., 1958. — The ecology of *Eucalyptus regnans* F. Muell.: The species and its frost resistance. *Aust. J. Botany* 6: 154-176.

——, 1981. — Fire in tall open forests (Wet Sclerophyll Forests). *In* GILL, A. M., GROVES, A. H., and NOBLE, I. R., (eds), *Fire and the Australian Biota*: 339-366. Canberra: Australian Academy of Science.

BAKER, R. T., 1889. — On three new species of *Eucalyptus. Proc. Linn. Soc. N.S.W.* 24: 596.

——, 1919. — *The Hardwoods of Australia and their Economics.* Sydney: Government Printer.

BEADLE, N. C. W., 1954. — Soil phosphate and the delimitation of plant communities in eastern Australia. *Ecology* 35: 370-375.

——, 1962. — Soil phosphate and the delimitation of plant communities in eastern Australia. 2. *Ecology* 43: 282-288.

BOLAND, D. J., BROOKER, M. I. H., CHIPPENDALE, G. M., HALL, N., HYLAND, B. P. M., JOHNSTON, R. D., KLEINIG, D. A., and TURNER, J. D., 1984. — *Forest Trees of Australia.* Commonwealth Scientific and Industrial Research Organisation, Australia.

BROUGH, P., MCLUCKIE, J., and PETRIE, A. H. K., 1924. — An ecological study of the flora of Mt Wilson. I. The vegetation of the basalt. *Proc. Linn. Soc. N.S.W.* 49: 475-498.

CUNNINGHAM, T. M., 1960. — The natural regeneration of *Eucalyptus regnans.* School of Forestry, University of Melbourne, Bull. No 1.

FORSTER, G. R., CAMPBELL, D., BENSON, D., and MOORE, R., 1977. — Vegetation and soils of the western region of Sydney. CSIRO Division of Land Use, Canberra. Technical Memorandum 77/10.

GILBERT, J. M., 1959. — Forest succession in the Florentine Valley. *Pap. Proc. Roy. Soc. Tasmania* 93: 129-151.

JACKSON, W. D., 1968. — Fire, air, water and earth; an elemental ecology of Tasmania. *Proc. Ecol. Soc. Aust.* 3: 9-16.

PECOVER, S. R., 1984. — Friable sandstone of the Sydney basin — a major source of industrial and construction sand for the Sydney market. Geoscience in the Development of Natural Resources, *Geol. Soc. Aust., Abstracts* No 12: 430-432.

PETRIE, A. H. K., 1925. — An ecological study of the flora of Mt Wilson. II. The Eucalyptus forests. *Proc. Linn. Soc. N.S.W.* 50: 145-166.

PIDGEON, I. M., 1937. — The ecology of the central coastal area of New South Wales. I. The environment and general features of the vegetation. *Proc. Linn. Soc. N.S.W.* 62: 315-340.

——, 1938. — The ecology of the central coastal area of New South Wales. II. Plant succession on the Hawkesbury Sandstone. *Proc. Linn. Soc. N.S.W.* 63: 1-26.

——, 1940. — The ecology of the central coastal area of New South Wales. III. Types of primary succession. *Proc. Linn. Soc. N.S.W.* 65: 221-249.

POLLARD, J. H., 1977. — *A Handbook of Numerical and Statistical Techniques.* Cambridge: Cambridge University Press.

Distribution and Ecology of Recent Ostracodes (Crustacea) from Port Hacking, New South Wales

I. YASSINI and A. J. WRIGHT

YASSINI, I., & WRIGHT, A. J. Distribution and ecology of Recent ostracodes from Port Hacking, New South Wales. *Proc. Linn. Soc. N.S.W.* 110 (2), (1987) 1988: 159-174.

Thirty-three species of Recent ostracodes from Port Hacking are documented, including *Hemicytheridea hiltoni* Yassini sp.nov. and *Semicytherura illerti* Yassini sp. nov. described herein. In the marine zone in Gunnamatta Bay, thirty species are present and the fauna is dominated by *Paracytheroma sudaustralis* (McKenzie) and *Callistocythere dorsotuberculata paucicostata* Yassini and Jones. Twenty-one species occur in the tidal zone of South West Arm, with '*Hiltermannicythere' bassiounii* Hartmann and *Loxoconcha australis* Brady the dominant species.

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INTRODUCTION

Port Hacking is an estuary located about 18km south of the city of Sydney on the central coast of New South Wales (Fig. 1). It is a drowned river valley (Chapman *et al.*, 1982) with a deep water entrance. The estuary was formed by the drowning of the Hacking River valley during the postglacial marine transgression.

Hacking River drains a catchment of Triassic rocks, being located in an incised 11km dendritic valley, and enters the Port Hacking embayment. Ocean waves contribute to the sediment distribution at the mouth of the estuary and up to 5km upstream.

Coarse sandy and silty marine sediments are mainly deposited near the mouth. In the main basin silty sand and mud occur in the shallow tidal flat deposits (Chapman *et al.*, 1982).

Prior to the present work, no published information on the species spectrum and distribution of ostracodes in the estuary was available. The aim of this paper and forthcoming publications is to provide an account of ostracode diversity and distribution in the estuarine and lagoonal environments of the central and southern coasts of New South Wales.

This paper in particular adds to the sparse information available and focuses attention on stratified environments which are at times (see below) oxygen-poor. Contributions covering other environments will further add to our understanding of ostracode ecology. Some data on a major coastal New South Wales lagoon (Lake Illawarra) have been provided by Yassini and Jones (1987).

ENVIRONMENTAL FACTORS

The physical and chemical environmental parameters of Port Hacking have been intensively investigated by the Division of Fisheries and Oceanography of CSIRO for the period 1953 to 1962 (Newell, 1966) and also 1975 (Scott, 1978).

Figure 2 shows the seasonal variation in salinity, temperature and dissolved oxygen at South West Arm Station in 1975 (Scott, 1978, figs 1, 2) where the mid-tide depth was 20m. The mean water surface temperature (Fig. 2**a**) had an annual variation from 14.8° (July) to 22.5°C (in February). The salinity ranged from less than 30‰ to more than 35‰ (Fig. 2**b**). During heavy rain periods in March, April and June of 1975 clear

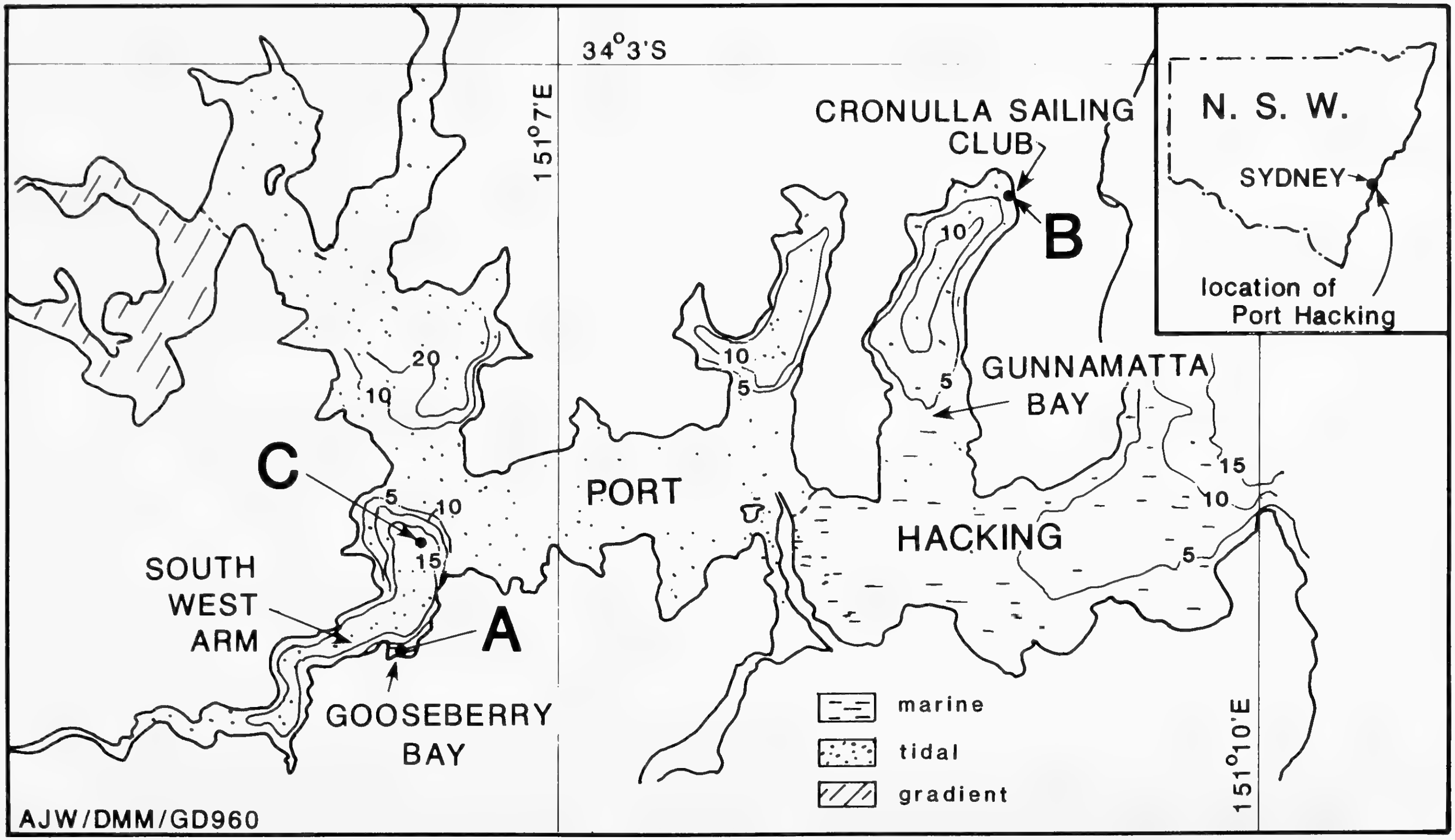

Fig. 1. Locality diagram of Port Hacking, New South Wales. Samples taken from two sections (A and B — see Figs 3 and 4). CSIRO data (see Fig. 2) collected at locality C (Scott, 1978). Depths for some parts only of Port Hacking are given in metres after 1:25,000 Botany Bay and Port Hacking naval map, 1982 (2nd edition). Three zones of circulation (after Rochford, 1951, 1959) are shown, these being (1) marine, (2) tidal and (3) gradient.

stratification in salinity was observed in South West Arm. The stratification in the water column during November and December was caused by the temperature difference between the surface and bottom.

The period of stratification was accompanied by deoxygenation of the water column below 10m (Fig. 2**c**) and in March the dissolved oxygen concentration decreased to 25% of saturation (Scott, 1978). The phenomenon of temporary deoxygenation of the water in Port Hacking is also discussed by Godfrey and Parslow (1976). Rochford (1951, 1959) subdivided the estuary, on the basis of tidally controlled salinity changes, into three zones — marine, tidal and gradient (see Fig. 1).

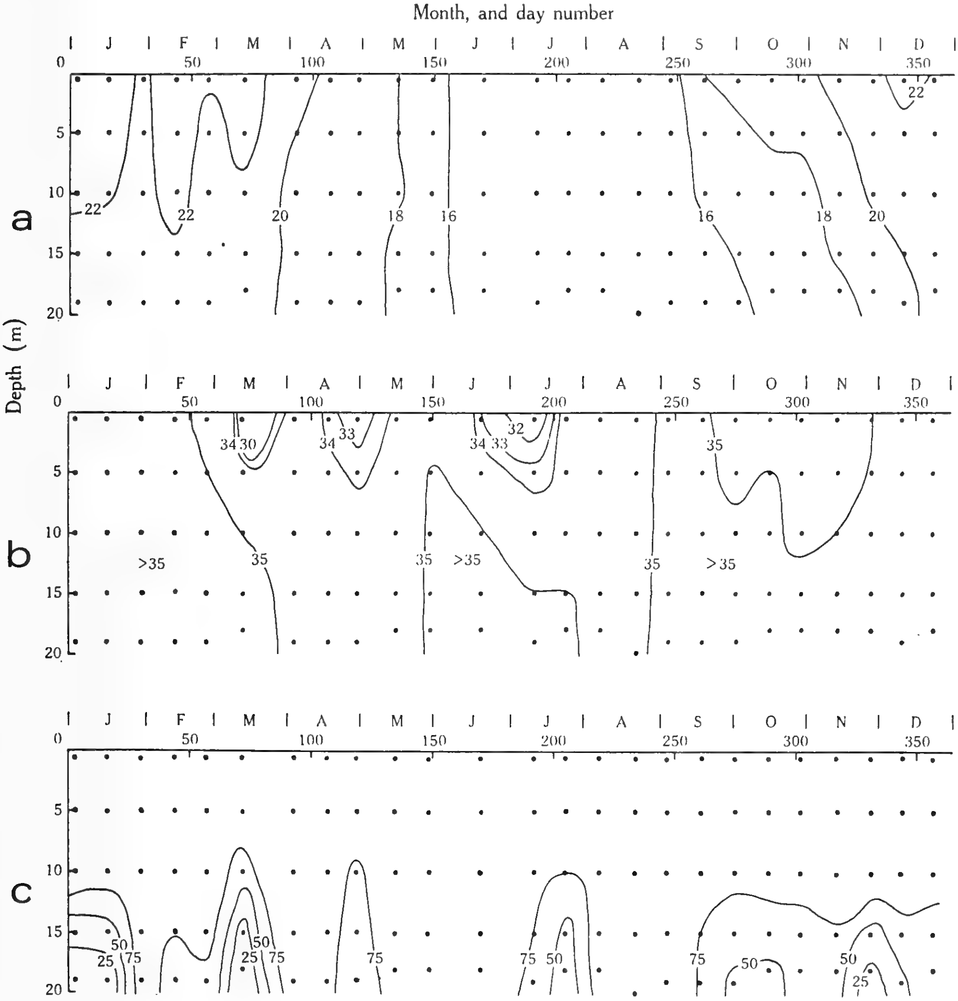

Fig. 2. Seasonal variation in Port Hacking waters, measured at locality C in South West Arm in 1975. (**a**) temperature (°C); (**b**) salinity ‰; and (**c**) dissolved oxygen (% saturation). All are plotted against depth in metres. Reproduced from Scott (1978) by permission.

METHODS AND MATERIAL

Samples were collected by SCUBA divers from South West Arm (tidal zone) from 2 to 10m depth (Fig. 3) and from 2 to 3m depth at the Cronulla Sailing Club, (*Posidonia* beds, Gunnamatta Bay marine zone) (Fig. 4). 500cc of fresh samples were sieved the same day and the residue dried in the oven. 50cc of the residue were treated with carbon tetrachloride. Counts of the number of ostracodes were based on both articulated and single valves. When found disarticulated, live specimens were identified by the presence of appendages inside the valve.

OSTRACODE FAUNAL ASSEMBLAGES

Figures 3 and 4 list the assemblages and give the proportions of dead and live shells in the ostracode populations encountered in South West Arm and Gunnamatta Bay respectively.

South West Arm lies in the tidal zone and Gunnamatta Bay in the marine zone (Fig. 1). This is reflected in the faunas, as there are 30 species recorded here from Gunnamatta Bay and 21 from South West Arm, of which 18 species are shared. Major differences in the assemblages can be seen (Figs 3, 4), in composition as well as diversity. In the tidal South West Arm (Fig. 3), *'Hiltermannicythere' bassiounii* Hartmann and *Loxoconcha australis* Brady are dominant, constituting 41% of the assemblages. The Gunnamatta Bay (Fig. 4) marine assemblage is dominated by three taxa constituting 53% of the assemblage; these are *Paracytheroma sudaustralis* (McKenzie), *Osticythere baragwanathi* (Chapman and Crespin), and *Callistocythere dorsotuberculata paucicostata* Yassini and Jones. *'H.' bassiounii* is represented by only a few isolated valves in Gunnamatta Bay despite its dominance (43-45%) in South West Arm. *O. baragwanathi* is present in both localities but the proportion of living specimens is much higher in South West Arm.

O. baragwanathi and *P. sudaustralis* are typical inhabitants of coastal barrier lagoons, where the salinity is highly fluctuating, and deoxygenation at the sediment-water interface often occurs as a result of salinity stratification, especially as a result of major flooding (State Pollution Control Commission (N.S.W.), 1983; Gibbs, 1986). In Lake Illawarra, where the average salinity range is 15-47‰, these two species constitute 92% of the ostracode fauna on the muddy substrate of the lake. Elsewhere in New South Wales, other coastal lagoons possess these species. In Narrabeen Lagoon, as well as Brisbane Water, *O. baragwanathi* is the most abundant faunal element in muddy substrates. In Tuggerah Lake, *O. baragwanathi* and *P. sudaustralis* are the predominant ostracode species. In Lake Macquarie an assemblage of *O. baragwanathi*, *Pectocythere portjacksonensis*, *P. sudaustralis* and *Hemicytheridea hiltoni* forms 90% of the ostracode fauna in muddy substrates. By contrast, in open bays such as Jervis Bay and Twofold Bay, and estuaries with large ocean exchanges (Hawkesbury River), these species are absent or quite subordinate.

Comparison of the ostracode fauna of Port Hacking with those of other estuaries indicates that it is intermediate between a typical lagoon fauna and that known from open bays or drowned valley estuaries such as Jervis Bay and Broken Bay.

In summary, a total of 33 species belonging to 23 genera are identified in the studied materials for both faunas. Two new species, *Hemicytheridea hiltoni* and *Semicytherura illerti* are described. A short synonymy list with most recent references is given for the other species. Two species listed in Fig. 4 (*Callistocythere* sp. nov. and *Loxoconcha* sp. nov.) are not illustrated herein or mentioned in the text, as they are rare and will be described on the basis of abundant material from Botany Bay, a few kilometres to the north of Port Hacking. Equally, rare material referred to *Bairdoppilata* sp. (Fig. 4) is

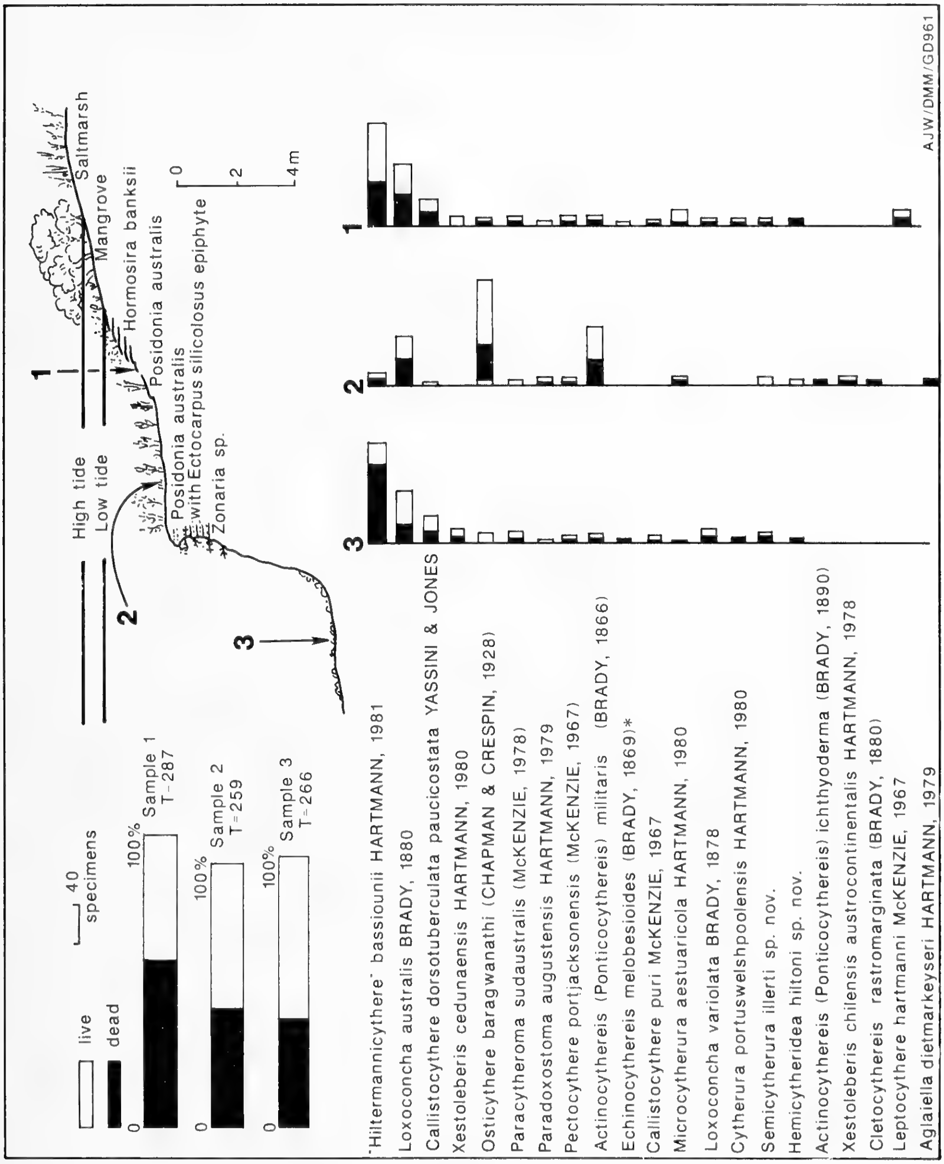

Fig. 3. Distribution of ostracodes in tidal zone in South West Arm, Port Hacking (locality A of Fig. 1). T is total number of individuals per 50cc of washed residue. Proportion of dead specimens in sample 1 (T = 287) is 58%; in sample 2 (T = 259) is 45%; and in sample 3 (T = 266) is 40%. Near-shore profile showing associated flora gives location of samples. In top left of diagram, proportion of dead specimens is shown in black. Asterisk indicates juvenile specimens.

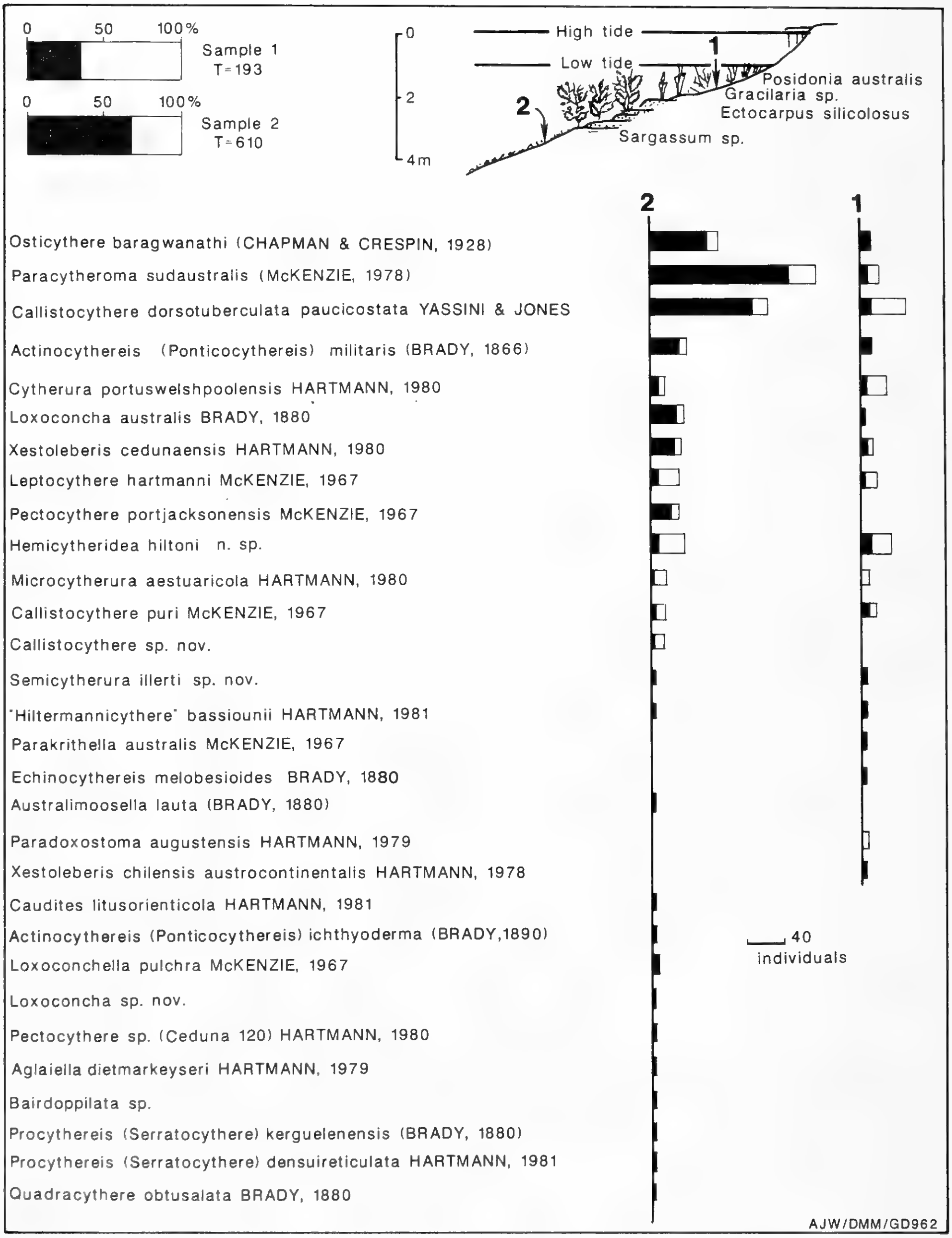

Fig. 4. Distribution of ostracodes in profile off jetty at Cronulla Sailing Club, Gunnamatta Bay (locality B of Fig. 1), in marine zone of circulation. T is total number of individuals per 50cc of washed residue. Proportion of dead specimens in sample 1 is 35% (T = 193) and in sample 2 is 67% (T = 610). Nearshore profile showing associated floras gives location of samples. In top left of diagram, proportion of dead specimens is shown in black.

neither illustrated nor mentioned in the text. *Australimoosella lauta* (Brady), *Pectocythere* sp. (Ceduna 120), *Procythereis (Serratocythere) densuireticulata* Hartmann, *P. (S.) kerguelenensis* (Brady), *Quadracythere obtusalata* (Brady) and *Loxoconchella pulchra* McKenzie are not illustrated. All specimens are deposited at the Australian Museum; AMP refers to specimens in the Recent Crustacea catalogue. All photographs are by SEM,and each is provided with a linear scale.

SYSTEMATICS

Suborder PLATYCOPIDA

Family BAIRDIIDAE Brady, 1883

Genus *Bairdoppilata* Corywell, Sample and Jennings, 1935

Bairdoppilata sp.

(AM P36478)

Only two isolated valves of this form were encountered in Gunnamatta Bay and are not illustrated.

Family CYTHERIDAE Baird, 1850

Genus *Microcytherura* Müller, 1894

Microcytherura aestuaricola Hartmann

(Fig. 5**G-I**) (AM P36493)

1980 *Microcytherura aestuaricola* Hartmann, p.117, pl.3, figs 7-13

Family OSTICYTHERIDAE Hartmann, 1980

Genus *Osticythere* Hartmann, 1980

Osticythere baragwanathi (Chapman and Crespin)

(Fig. 5**M,N**) (AM P36494)

1928 *Cythere baragwanathi* Chapman and Crespin, p.126, pl.10, fig. 65a,b
1980 *Osticythere reticulata* Hartmann, p.119, pl.4, fig. 7-18
1984 *Osticythere reticulata* Hartmann; McKenzie and Pickett, p.236, fig. 4, R-U
1986 *Osticythere baragwanathi* (Chapman and Crespin); McKenzie, p.107

Family LEPTOCYTHERIDAE Hanai, 1957

Genus *Leptocythere* Sars, 1928

Leptocythere hartmanni (McKenzie)

(Fig. 7**K,L**) (AM P36489)

1967 *Callistocythere hartmanni* McKenzie, p.81, pl.12, fig. 5
1978 *Leptocythere hartmanni* (McKenzie); Hartmann, p.79, figs 101-107
1980 *Leptocythere hartmanni* (McKenzie); Hartmann, p.123, pl.5, figs 15,16,18,19
1984 *Callistocythere hartmanni* McKenzie; McKenzie and Pickett, p.239, fig. 5Y

Genus *Callistocythere* Ruggieri, 1953

Callistocythere dorsotuberculata paucicostata Yassini and Jones

(Fig. 7**M,N**) (AM P36479)

1987 *Callistocythere dorsotuberculata paucicostata* Yassini and Jones, p.27, pl.2, figs 3-4

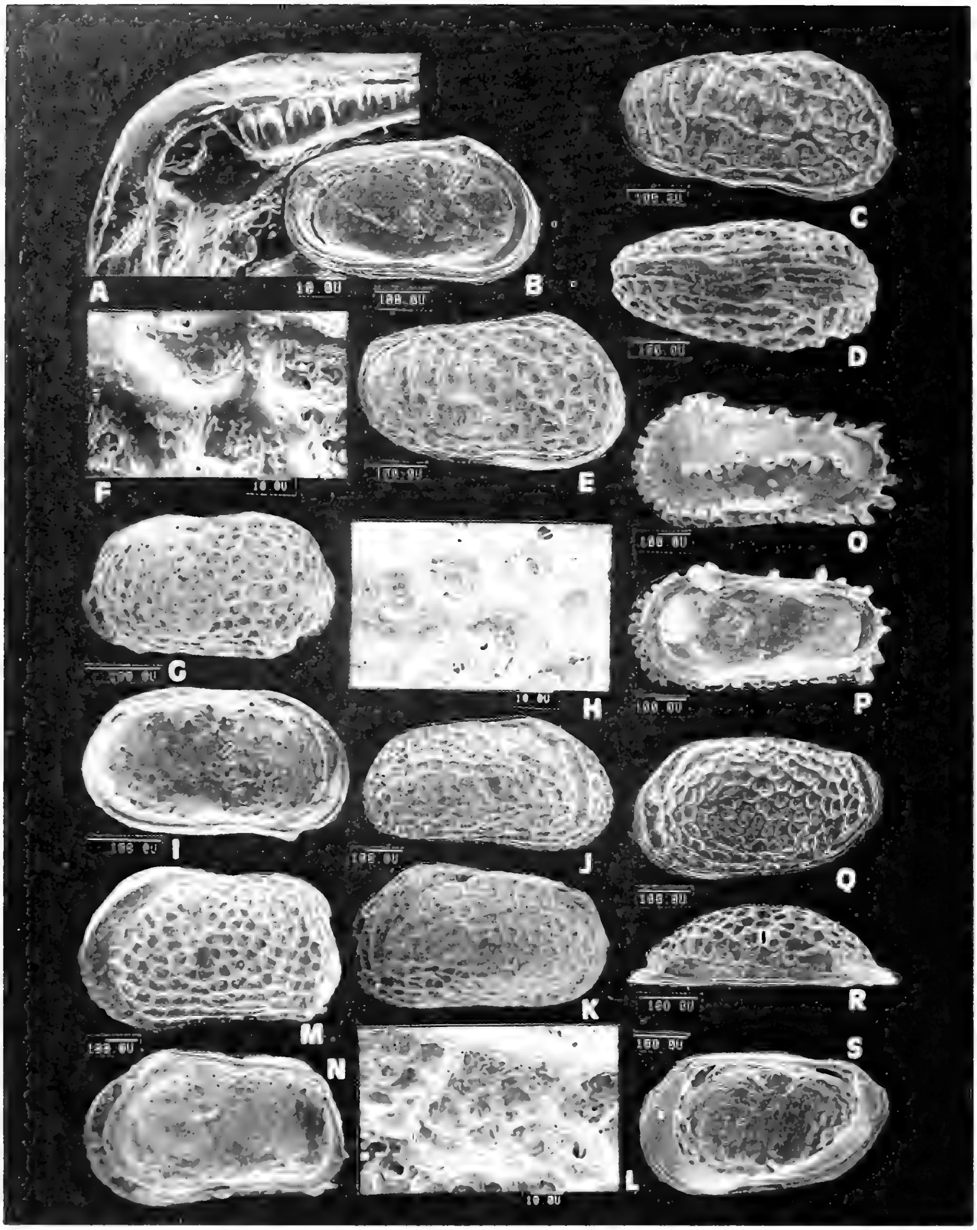

Fig. 5. **A-F**, *Hemicytheridea hiltoni* Yassini sp.nov. **A**, LV with details of posterior hinge teeth and sockets; **B**, LV internal view; **C**, RV external view, *holotype*; **D**, Ventral view of carapace; **E**, RV external view; **F**, Details of ornamentation. Sample 2, Port Hacking, Gunnamatta Bay. **G-I**, *Microcytherura aestuaricola* Hartmann, 1980. **G**, LV external view; **H**, Details of ornamentation; **I**, LV internal view. Sample 2, Port Hacking, South West Arm. **J-L**. *'Hiltermannicythere' bassiounii* Hartmann, 1981. **J**, RV external view; **K** (same scale as **J**), LV external view; **L**, Details of ornamentation. Sample 2, Port Hacking, South West Arm. **M, N**, *Osticythere baragwanathi* (Chapman and Crespin, 1928). **M**, LV external view; **N**, RV internal view. Sample 3, Port Hacking, South West Arm. **O, P**, *Actinocythereis (Ponticocythereis) militaris* (Brady, 1866). **O**, LV external view; **P**, internal view. Sample 3, Port Hacking, South West Arm. **Q-S**, *Loxoconcha variolata* Brady, 1878. **Q**, LV external view; **R**, LV dorsal view; **S**, RV internal view. Sample 1, Port Hacking, South West Arm.

Callistocythere puri McKenzie
(Fig. 7**O**) (AM P36480)

1967 *Callistocythere puri* McKenzie, p.81, pl.12, fig. 2; text-fig. 32
1980 *Callistocythere puri* McKenzie; Hartmann, p.124, pl.7, figs 3,6

Family CYTHEROMIDAE Elofson, 1939
Genus *Paracytheroma* Juday, 1907

Paracytheroma sudaustralis (McKenzie)
(Fig. 7**C,D**) (AM P36495)

1978 *Cytheroma sudaustralis* McKenzie, p.178, figs 30,35-42
1980 *Paracytheroma sudaustralis* (McKenzie); Hartmann, p.128, figs 51-56

Genus *Parakrithella* Hanai, 1959

Parakrithella australis McKenzie
(Fig. 7**G**) (AM P36497)

1967 *Parakrithella australis* McKenzie, p.72, pl.26 fig. N-O
1980 *Parakrithella* cf. *australis* McKenzie; Hartmann, p.129
1984 *Parakrithella australis* McKenzie; McKenzie and Pickett, p.236, fig. 4G-H

Family TRACHYLEBERIDIDAE Sylvester-Bradley, 1948
Genus *Actinocythereis* Puri, 1953
Subgenus *Ponticocythereis* McKenzie, 1967

Actinocythereis (Ponticocythereis) militaris (Brady)
(Fig. 5**O,P**) (AM P36476)

1866 *Cythereis militaris* Brady, p.385, pl.61, fig. 9a-d
1880 *Cythere clavigera* Brady, p.111, pl.23, fig. 7a-d
1967 *Ponticocythereis militaris* (Brady); McKenzie, p.96, pl.3, fig. 4, text-figs 40 and 10c-d
1976 *Cythere clavigera* Brady; Puri and Hulings, p.270, pl.16, figs 1,2, text-fig. 4
1984 *Ponticocythereis militaris* (Brady); McKenzie and Pickett, p.239, fig. 5B

Actinocythereis (Ponticocythereis) ichthyoderma Brady
(Fig. 6**E,F**) (AM P36483)

1890 *Cythere ichthyoderma* Brady, p.503, pl.2, figs 22,23
1986 *Ponticocythereis quadriserialis* Brady; McKenzie, p.98, pl.2, fig. 13

Genus *Australimoosella* Hartmann, 1978

Australimoosella lauta (Brady)

1880 *Cythere lauta* Brady, p.88, pl.21, fig. 4a-d
1976 *Cythere lauta* Brady; Puri and Hulings, p.280, pl.4, figs 5-8

Genus *Hiltermannicythere* Bassiouni, 1970

'Hiltermannicythere' bassiounii Hartmann
(Fig. 5**J-L**) (AM P36488)

1978 *Hiltermannicythere bassiounii* Hartmann, p.91, pl.7, figs 6-14
1979 *Hiltermannicythere bassiounii*; Hartmann, p.232, pl.5, figs 10-20
1980 *Hiltermannicythere bassiounii*; Hartmann, p.131, pl.9, figs 8-11, 13-14

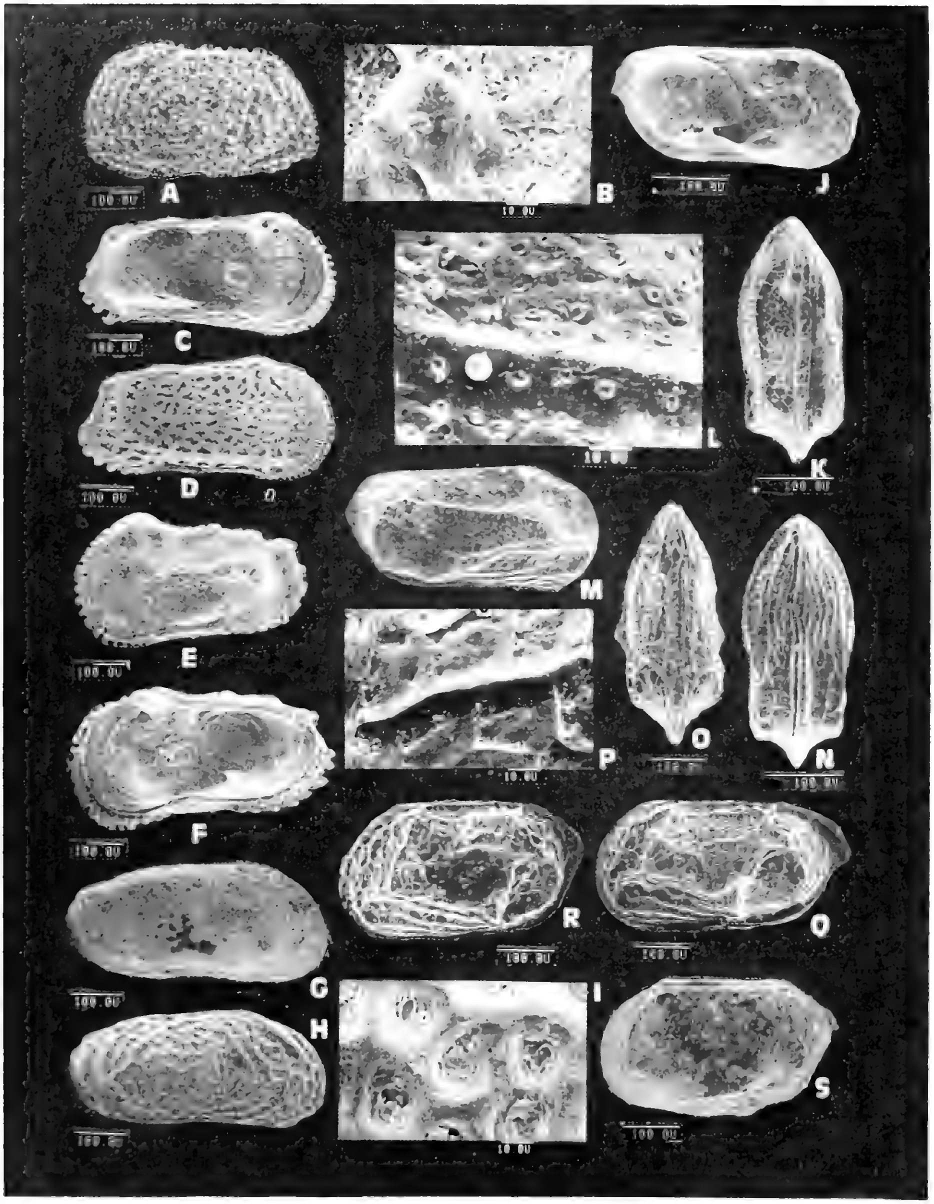

Fig.6. **A**, **B**, *Echinocythereis melobesioides* (Brady, 1880). **A**, LV external view; **B**, details of ornamentation. Sample 3, Port Hacking, South West Arm. **C**, **D**, *Cletocythereis rastromarginata* (Brady, 1880). **C**, LV internal view; **D**, RV external view. Sample 2, Port Hacking, South West Arm. **E**, **F**, *Actinocythereis (Ponticocythereis) ichthyoderma* (Brady, 1890). **E**, LV external view; **F**, RV internal view. Sample 2, Port Hacking, Gunnamatta Bay. **G-I**, *Pectocythere portjacksonensis* (McKenzie, 1967), **G**, LV internal view; **H**, RV external view; **I**, details of ornamentation. Sample 2, Port Hacking, Gunnamatta Bay. **J-N**, *Semicytherura illerti* Yassini n.sp. **J**, LV internal view; **K**, dorsal view of carapace; **L**, details of ornamentation, *holotype*; **M**, RV external view, *holotype*; **N** (same scale as **M**), ventral view of carapace. Sample 1, Port Hacking, South West Arm. **O-S**, *Cytherura portuswelshpoolensis* Hartmann, 1980. **O**, dorsal view of carapace; **P**, details of ornamentation; **Q**, LV external view; **R**, LV external view; **S**, RV internal view. Sample 1, Port Hacking, Gunnamatta Bay.

Genus *Echinocythereis* Puri, 1953

Echinocythereis melobesioides (Brady)
(Fig. 6**A,B**) (AM P36485)

1880 *Cythere melobesioides* Brady, p.108, pl.18, fig. 1a-g
1976 *Cythere melobesioides* Brady; Puri and Hulings, pl.25, figs 1-2

Family HEMICYTHERIDAE Puri, 1953

Genus *Cletocythereis* Swain, 1963

Cletocythereis rastromarginata (Brady)
(Fig. 6**C-D**) (AM P36482)

1880 *Cythere rastromarginata* Brady, p.83, pl.16, fig. 1a-d
1967 *Cletocythereis rastromarginata* (Brady); McKenzie, p.95, pl.13, figs 1-2
1979 *Cletocythereis* cf. *rastromarginata* (Brady): Hartmann, p.234, pl.6, figs 5-7
1984 *Cletocythereis rastromarginata* (Brady); McKenzie and Pickett, p.239, fig. 5C-D

Genus *Quadricythere* Hornibrook, 1952

Quadricythere obtusalata (Brady, 1880)

1880 *Cythere obtusalata* Brady, p.91, pl.12, fig. 1a-c
1976 *Cythere obtusalata* Brady; Puri and Hulings, p.282, pl.5, figs 10-12

Genus *Procythereis* Skogsberg, 1928

Subgenus *Serratocythere* Hartmann, 1979

Procythereis (Serratocythere) densuireticulata Hartmann
(AM P36500)

1981 *Procythereis (Serratocythere) densuireticulata* Hartmann, p.110, pl.7, figs 3-9
1982 *Procythereis (Serratocythere) lyttletonensis* Hartmann, p.131, pl.5, figs 6-11

Procythereis (Serratocythere) kerguelenensis (Brady)
(AM P36501)

1880 *Cythere kerguelenensis* Brady, p.78-79, pl.4, figs 16-18; pl.20, fig. 1a-f
1974 *'Hemicythere' kerguelenensis* (Brady); McKenzie, p.160, pl.1, fig. 9
1981 *Procythereis (Serratocythere) australis* Hartmann, p.110, pl.7, figs 1-2

Genus *Caudites* Coryell and Fields, 1937

Caudites litusorienticola Hartmann
(Fig. 7**H**) (AM P36481)

1981 *Caudites litusorienticola* Hartmann, p.111, pl.7, figs 10-13

Family LOXOCONCHIDAE Sars, 1925

Genus *Loxoconcha* Sars, 1868

Loxoconcha australis Brady
(Fig. 7**P**) (AM P36490)

1880 *Loxoconcha australis* Brady, p.119, pl.28, fig. 3a-d, fig. 5a-f
1967 *Loxoconcha australis* Brady; McKenzie, p.86, pl.12, figs 10-11, fig. 3n-o

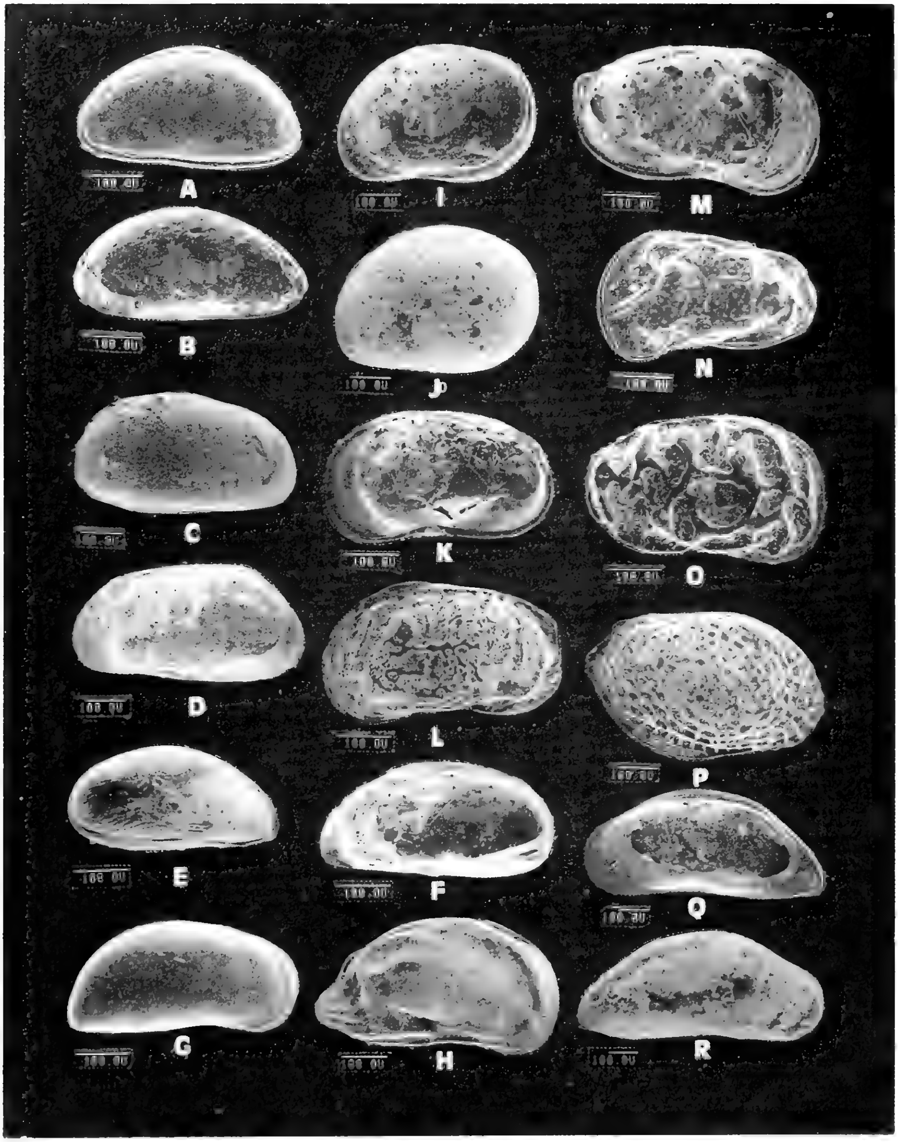

Fig. 7. **A**, **B**, *Paradoxostoma augustensis* Hartmann, 1979. **A**, LV external view; **B**, RV internal view. Sample 2, Port Hacking, South West Arm. **C**, **D**, *Paracytheroma sudaustralis* (McKenzie, 1978). **C**, RV external view; **D**, RV internal view. Sample 2, Port Hacking, Gunnamatta Bay. **E**, **F**, *Xestoleberis chilensis austrocontinentalis* Hartmann, 1978. **E**, RV external view; **F**, RV internal view. Sample 1, Port Hacking, Gunnamatta Bay. **G**, *Parakrithella australis* McKenzie, 1967. **G**. RV external view. Sample 1, Port Hacking, Gunnamatta Bay. **H**, *Caudites litusorienticola* Hartmann, 1981. **H**, RV external view. Sample 2, Port Hacking, Gunnamatta Bay. **I**, **J**, *Xestoleberis cedunaensis* Hartmann, 1980. **I**, RV internal view; **J**, LV external view. Sample 2, Port Hacking, Gunnamatta Bay. **K**, **L**, *Leptocythere hartmanni* (McKenzie, 1967). **K**. RV internal view; **L**, LV external view. Sample 2, Port Hacking, Gunnamatta Bay. **M**, **N**, *Callistocythere dorsotuberculata paucicostata* Yassini and Jones. **M**, LV internal view; **N**, LV external view. Sample 2, Port Hacking, Gunnamatta Bay. **O**, *Callistocythere puri* McKenzie, 1967. **O**, RV external view. Sample 2, Port Hacking, Gunnamatta Bay. **P**, *Loxoconcha australis* Brady, 1880. **P**. RV external view. Sample 2, Port Hacking, Gunnamatta Bay. **Q**, **R**, *Aglaiella dietmarkeyseri* Hartmann, 1979. **Q**, RV internal view; **R**, RV external view. Sample 2, Port Hacking, Gunnamatta Bay.

Loxoconcha variolata Brady
(Fig. 5**Q-S**) (AM P36491)

1878 *Loxoconcha variolata* Brady, p.400, pl.18, fig. 4a-d
1880 *Loxoconcha variolata*; Brady, p.121, pl.29, fig. 6a-d

Genus *Loxoconchella* Triebel, 1954

Loxoconchella pulchra McKenzie
(AM P36492)

1967 *Loxoconchella pulchra* McKenzie, p.88, fig. 4c
1980 *Loxonchella* cf. *pulchra* McKenzie; Hartmann, p.140, pl.12, fig. 1
1984 *Loxonchella pulchra* McKenzie; McKenzie and Pickett, p.236, fig. 4A-B

Genus *Hemicytheridea* Kingma, 1948

Hemicytheridea hiltoni Yassini, sp.nov.
(Fig. 5**A-F**) (AM P36486-36487)

Derivation of name: for Mr Neville Hilton, chairman of the Lake Illawarra Management Committee
Holotype: one right valve AM P36486
Paratypes: 2 carapaces and one left valve AM P36487
Type Stratum: Recent; sandy mud with *Posidonia australis*
Type Locality: Gunnamatta Bay, Port Hacking estuary
Dimensions: Holotype length 225μ; width 115μ
Paratype length 205-230μ; width 100-115μ
Description: Carapace small elongate, subreniform; dorsal margin straight. Ventral margin slightly sinuous in anteroventral portion, anterior margin broadly rounded.
Posterior end subacute with distinct postero-dorsal cardinal angle. Inner lamella moderately wide at anterior end, narrows at posterior margin. Narrow vestibulum present at both margins. Marginal pore canals straight, about 20 at anterior margin and 11 at the posterior margin.
Surface of valve with strongly reticulate ornament, with prominent rib running obliquely from postero-median area to antero-ventral region. Two vertical ridges running from dorsal to ventral margin present at posterior end.
Wrinkled structure on surface of reticulation observed at high magnification. Sexual dimorphism present, the male being slightly longer and narrower than the female.
Remarks: Hinge structure and muscle scars are characteristic of *Hemicytheridea*. The species is close to *Hemicytheridea crenata* (Brady, 1890) but the latter mainly differs by having much more pronounced vertical ridges all over the surface of the valves.

Family PECTOCYTHERIDAE Hanai, 1957
Genus *Pectocythere* Hanai, 1957

Pectocythere portjacksonensis (McKenzie)
(Fig. 6**G-I**) (AM P36498)

1967 *'Hemicytheridea' portjacksonensis* McKenzie, p.85, fig. 3i-j; pl.12, fig. 6
1980 *'Pectocythere' portjacksonensis* (McKenzie); Hartmann, p.122, pl.5, fig. 17

Pectocythere sp. (Ceduna 120) Hartmann, 1980
(AM P36499)

1980 *Pectocythere* sp. (Ceduna 120) Hartmann, p.123, pl.3, figs 14-17

Family CYTHERURIDAE Müller, 1894

Genus *Cytherura* Sars, 1866

Cytherura portuswelshpoolensis Hartmann

(Fig. 6**O-S**) (AM P36484)

1980 *Cytherura portuswelshpoolensis* Hartmann, p.140, pl.12, figs 2-3
1981 *Cytherura portuswelshpoolensis* Hartmann, p.121
1984 Cytherurid sp.; McKenzie and Pickett, p.236, fig. 4E

Genus *Semicytherura* Wagner, 1957

Semicytherura illerti Yassini, sp.nov.

(Fig. 6**J-N**) (AM P36502-36503)

Derivation of name: for Mr Chris Illert, who provided the samples for this study
Holotype: a right valve of a male, AM P36502
Paratypes: two carapaces and one left valve, AM P36503
Type Stratum: Recent; sandy mud with *Posidonia australis*
Type Locality: South West Arm, Port Hacking estuary
Dimensions: holotype length 170μ; width 182μ
paratype length 170-180μ; width 75-85μ

Description: Carapace medium size, elongate subrectangular, with subdorsal weakly developed caudal process. Dorsal margin straight, ventral margin slight sinuous in the middle. Anterior border well rounded in dorsal view.

Carapace is parallel-sided and acuminate at the extremities. Surface of valve with one prominent medio-dorsal longitudinal ridge and two or three medio-ventral ridges. Network of intercostal reticulation well developed at the anterior and posterior part of the valves. Intercostal area finely punctate. In ventral view four to five subparallel weakly developed ridges present. Eye tubercle prominent.

Inner lamella very wide both anteriorly and posteriorly, curving forms forward strongly in central part of valve.

Remarks: Such hinge structures and muscle scars are characteristic of *Semicytherura*. Sexual dimorphism is pronounced, the male carapace being much longer and narrower than the female.

Family XESTOLEBERIDIDAE

Genus *Xestoleberis* Sars, 1866

Xestoleberis cedunaensis Hartmann

(Fig. 7**I,J**) (AM P36504)

1980 *Xestoleberis cedunaensis* Hartmann, p.149, pl.15, figs 1-4
1984 *Xestoleberis cedunaensis* Hartmann; McKenzie and Pickett, p.239, text-fig. 5Q-S

Xestoleberis chilensis austrocontinentalis Hartmann

(Fig. 7**E,F**) (AM P36505)

1978 *Xestoleberis chilensis austrocontinentalis* Hartmann, p.128, figs 461-464
1981 *Xestoleberis chilensis austrocontinentalis* Hartmann, p.122, pl.11, figs 1-12

Family PARADOXOSTOMIDAE Brady and Norman, 1889

Genus *Paradoxostoma* Fischer, 1855

Paradoxostoma augustensis Hartmann
(Fig. 7**A,B**) (AM P36496)

1979 *Paradoxostoma augustensis* Hartmann, p.261, text-figs 188-192
1980 *Paradoxostoma augustensis* Hartmann, p.157

Family CANDONIDAE Kaufmann, 1900
Genus *Aglaiella* Daday, 1910

Aglaiella dietmarkeyseri Hartmann
(Fig. 7**Q,R**) (AM P36477)

1979 *Aglaiella dietmarkeyseri* Hartmann, p.264, text-figs 241-250

ACKNOWLEDGEMENTS

We thank C. Illert for providing the samples, Mrs Anne Clarke and the Lake Illawarra Management Committee for their support, Therese Carmody who typed the manuscript and David Martin who drafted the figures. The work was supported by a 1986 grant from the University of Wollongong Research Committee. SEM facilities were kindly provided by the Electron Microscope Unit, University of Sydney.

References

BRADY, G. S., 1866. — On new or imperfectly known species of marine *Ostracoda*. *Trans zool. Soc. Lond.* 5: 359-93.

——, 1878. — A monograph of the *Ostracoda* of the Antwerp Crag. *Trans zool. Soc. Lond.* 10: 379-409.

——, 1880. — Report on the *Ostracoda* dredged by H.M.S. Challenger during the years 1873-1876. *Rept Voyage Challenger, Zool.* 1: 1-184.

——, 1890. — On *Ostracoda* collected by H. B. Brady in the South Sea Islands. *Trans Roy. Soc. Edinb.* 25: 489-524.

CHAPMAN, D. M., GEARY, M., ROY, P. S., and THOM, B. G., 1982. — *Coastal Evolution and Coastal Erosion in New South Wales*. A report prepared for the Coastal Councils of N.S.W. 340pp.

CHAPMAN, F., CRESPIN, I., and KEBLE, R. A., 1928. — The Sorrento Bore, Mornington Peninsula, with a description of new or little known fossils. *Rec. geol. Surv. Vict.* 5: 1-95.

GIBBS, P. J., 1986. — Five N.S.W. barrier lagoons; their macrobenthic fauna, seagrass communities. Kensington (N.S.W.): University of New South Wales, Ph.D. thesis, unpubl.

GODFREY, J. J., and PARSLOW, J., 1976. — Description and Preliminary Theory of Circulation in Port Hacking estuary. *C.S.I.R.O. Aust. Div. Fish. Oceanogr. Rept* 67.

HARTMANN, G., 1978. — Zur Kenntnis des Eulitorals der australischen küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitt. hamb. zool. Mus. Inst.* 75: 63-219.

——, 1979. — Die Ostracoden der Ordnung Podocopida G. W. Müller, 1894 der warmtemperierten (antiborealen) West- und Südwestküste Australiens (zwischen Perth im Norden und Eucla im Süden). *Mitt. hamb. zool. Mus. Inst.* 76: 219-301.

——, 1980. — Die Ostracoden der Ordnung Podocopida G. W. Müller, 1894 der warm-temperierten und subtropisch-tropischen Küstenabschnitte der Süd- und Südostkuste Australiens (zwischen Ceduna im Westen und Lakes Entrance im Osten). *Mitt. hamb. zool. Mus. Inst.* 77: 11-204.

——, 1981. — Die Ostracoden der Ordnung Podocopida G. W. Müller, 1894 der subtropisch-tropischen Ostkuste Australiens (zwischen Eden im Süden und Heron Island im Norden). *Mitt. hamb. zool. Mus. Inst.* 78: 97-149.

——, 1982. — Beitrag zur Ostracodenfauna Neueseelands (mit einem Nachtrag zur Ostracodenfauna der Westküste Australiens. *Mitt. hamb. zool. Mus. Inst.* 79: 119-50.

MCKENZIE, K. G., 1967. — Recent Ostracoda from Port Philip Bay, Victoria. *Proc. Roy. Soc. Vict.* 80: 61-106.

——, 1974. — Cenozoic Ostracoda of southeastern Australia with the description of *Hanaiceratina* new genus. *Geoscience and Man* 6: 153-82.

——, 1978. — Biogeographic patterns in Australian Cainozoic Ostracoda, with the description of *Orlovibairdia* new genus. *J. palaeont. Soc. India* 20: 279-88.

——, 1981. — Chapman's 'Mallee Bores' and 'Sorrento Bore' Ostracoda in the National Museum of Victoria, with the description of *Maddocksella* new genus. *Proc. Roy. Soc. Vict.* 93: 105-7.

——, 1986. — A comparative study of collections from the S.W. Pacific (Saipan to Tonga), with the description of *Gambiella caudata* Brady, 1890) and new species of *Pterobairdia (Ostracoda). J. Micropaleont.* 5: 91-108.

——, and PICKETT, J. W., 1984. — Environmental interpretations of Late Pleistocene ostracode assemblages from the Richmond River valley, New South Wales. *Proc. Roy. Soc. Vict.* 96: 227- 42.

NEWELL, B. S., 1966. — Seasonal changes in hydrological and biological environments of Port Hacking, Sydney. *Aust. J. mar. freshw. Res.* 17: 77-91.

PURI, H. S., and HULINGS, N. C., 1976. — Description of lectotypes of some ostracodes from the Challenger Expedition. *Bull. Brit. Mus. (Nat. Hist.), Zoology* 29: 251-315.

ROCHFORD, D. J., 1951. — Studies in Australian estuarine hydrology. I — Introduction and comparative features. *Aust. J. mar. freshw. Res.* 2: 1-116.

——, 1959. — Classification of Australian estuarine systems. *Arch. Oceanogr. Limnol.* Vol. II Supp I.

SCOTT, B. D., 1978. — Nutrient cycling and primary production in Port Hacking, New South Wales. *Aust. J. mar. fresh. Res.* 29: 803-15.

STATE POLLUTION CONTROL COMMISSION (N.S.W.), 1983. — *Environmental Audit of Lake Macquarie*, 138 p.

YASSINI, I., and JONES, B. G., 1987 . — *Ostracoda* in Lake Illawarra: environmental factors, assemblages and systematics. *Aust. J. mar. freshw. Res.* 38: 795-843.

APPENDIX

LIST OF SPECIMENS

36476	*Actinocythereis (Ponticocythereis) militaris*
36477	*Aglaiella dietmarkeyseri*
36478	*Bairdoppilata* sp.
36479	*Callistocythere dorsotuberculata paucicostata*
36480	*Callistocythere puri*
36481	*Caudites litusorienticola*
36482	*Cletocythereis rastromarginata*
36483	*Actinocythereis (Ponticocythereis) ichthyoderma*
36484	*Cytherura portuswelshpoolensis*
36485	*Echinocythereis melobesioides*
36486	*Hemicytheridea hiltoni* (holotype)
36487	*H. hiltoni* (paratypes)
36488	*'Hiltermannicythere' bassiounii*
36489	*Leptocythere hartmanni*
36490	*Loxoconcha australis*
36491	*L. variolata*
36492	*Loxoconchella pulchra*
36493	*Microcytherura aestuaricola*
36494	*Osticythere baragwanathi*
36495	*Paracytheroma sudaustralis*
36496	*Paradoxostoma augustensis*
36497	*Parakrithella australis*
36498	*Pectocythere portjackonensis*
36499	*P.* sp. (Ceduna 120)
36500	*Procythereis (Serratocythere) densuireticulata*
36501	*P. (S.) kerguelenensis*
36502	*Semicytherura illerti* (holotype)
36503	*S. illerti* (paratypes)
36504	*Xestoleberis cedunaensis*
36505	*X. chilensis austrocontinentalis*

A new Species of *Nitella* (Characeae) belonging to the Pluricellulate Species Group in Australia*

A. T. HOTCHKISS and K. IMAHORI

HOTCHKISS, A. T., & IMAHORI, K. A new species of *Nitella* (Characeae) belonging to the pluricellulate species group in Australia. *Proc. Linn. Soc. N.S.W.* 110 (2), (1987) 1988: 175-185.

A new species of *Nitella*, *Nitella woodii*, belonging to the pluricellulate species group in Australia, is described from the Nepean River, near Camden, New South Wales. The new species appears to be related to *Nitella cristata* and to *Nitella hookeri*, species endemic to the Australasian region.

A. T. Hotchkiss, Professor Emeritus, Department of Biology, University of Louisville, Louisville, Kentucky, 40292, U.S.A., and K. Imahori, Vice-President, Naruto University of Teacher Education, Takashima, Naruto-Shi, 772, Japan; *manuscript received 17 September 1986, accepted for publication 19 August 1987.*

INTRODUCTION

During the course of systematic observations of charophytes in the Nepean River near Camden, New South Wales through the year 1968, a robust form of *Nitella* was found which is described here as a new species, *Nitella woodii*. The first specimen, taken in March while dredging for *Chara australis* in a deep pool near the highway bridge north of Camden, was a sterile fragment of a large plant resembling *Nitella flexilis*. In April, studies were concentrated on abundant charophyte beds in the more accessible shallow pools above and below the highway bridge of the airport road west of Camden. A single bed of the new species was apparently restricted to the shaded cooler depths of a pool directly under the bridge. This is the type locality. While the plants in this bed remained sterile and without new growth for several months, all other nearby species, grew and fruited abundantly in beds scattered up and down the river. These included: *Chara australis*, *Nitella sonderi*, *Nitella penicillata*, *Nitella tasmanica*, *Nitella imahorii* and *Nitella cristata*, among dioecious species and *Chara gymnopitys*, *Nitella imperialis* and *Nitella horikawi*, among the monoecious forms.

Meanwhile, in the new species, peculiar vegetative, bud-like growths appeared and were studied from April until August. The growths showed possible dormancy and vegetative reproductive traits suggesting the designation of winter buds or turions. In early spring (late August), a burst of bright green new growth rooted in the bottom mud replaced the darkened, decaying older plants. New turions appeared on the new shoots and fruiting of male and female gametangia was abundant on separated plants from October into November. The late winter early spring appearance of this species suggests that it is markedly seasonal.

The bed of the Nepean River presents generally favourable substrate conditions for the growth of charophytes. Coming from a sandstone region, the river winds in the Camden area in a shallow sandy trough over sandbars mixed with varying degrees of organic muck. Periodically flooded, scoured and reshaped by water currents, the sandy bottom presents a dynamic substrate which charophytes are well able to exploit quickly. In 1968, conditions were optimal for the growth of charophytes. The recently-scoured river bed presented broad expanses of clean, sandy bottom. There was a good supply of

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* A paper presented at the International Seaweed Symposium, Santa Barbara, California, U.S.A., August 1977.

clean water in a shallow steady flow over rather broad shallow sandbars secure from competition from aquatic angiosperms along the shore. This favourable state continued through the following autumn, winter and into the spring when conditions slowly deteriorated partly as a result of encroaching sedges, silt and epiphytes, but mostly the result of the steadily lowering water level which left stretches of the river semistagnant and eventually in the grip of a drought, but not before the charophytes had produced an abundant crop of spores. In 1976 and in 1980, the first author revisited the site to find it under drought conditions. No collections could be made at either time.

OBSERVATIONS

Collections: Deep shaded pool, soft muddy bottom, under bridge, airport road, Nepean River, west of Camden, New South Wales.

A. T. Hotchkiss 68-3-13-2; 68-3-29-1 (observed in April); 68-6-29-2 (observed July, August); 68-10-5-1; 68-10-19-1; 68-11-3-1 (HOLOTYPE). Specimen, currently in University of Louisville Herbarium, will be transferred to the University of Sydney for disposition. Drawings made by K. Imahori from 68-10-19-1. Figs 1-13.

Diagnosis: *Nitella woodii A. T. Hotchkiss et K. Imahori.* Figs 1-13 *Nitella woodii* sp. nov. A. T. Hotchkiss et K. Imahori.

Planta dioecia, 30-100cm alta, viridis ad brunnea, gymnocarpa. Caulis robustus, 600-1250μ crassus; internodiis quam ramuli 2-plo longiora vel aequilonga. Verticilli steriles majores, ramulis 6, 2-3-tim furcatis, 8-11cm longi; radiis primarii totius longitudinis ramulorum 1/3-2/5, 2.5-4cm longi; radii secundarii 2-4, saepe cum ramulis accessoribus; radiis tertii 2-3; quaterni 2-3, abbreviati. Dactyli 2-3, (1-) 2-4 cellulati, inaequilongi; cellula ultima 55-100μ longa, ad basin 25-40μ lata.

Rami fertiles spiciformes ex apice vel axillari ramulorum secundari. Verticilli feminis quam masculi minus congesti vel similes; ramuli 6, 2-3 (-4) furcatis, 2-5.5cm longi; radii primarii totius longitudinis ramulorum 1/2-3/5; secundarii 3-4; tertii 3-4; quaterni 2-3, quorum 1 saepe in radiis quintis furcati. Dactyli 2-4, 2-3 cellulati; cellula ultima mucronata.

Gametangia ad nodos omnes exceptis primariis, solitaria. Antheridia 450μ longa et 420μ diametro. Oogonia brevi-stipitata, 675μ longa, 515μ lata; cellulae spirales 7-8; coronula parva, 35μ alta, cellula superiore quam inferiori 2-3 tim longiore, ad basin 50-55μ lata. Oospora fulva ad purpureo-brunnea, 515μ longa et 325μ lata; fossa 80μ lata; striis 5, paulum prominentibus. Membrana externa moniliformae; medius reticulata, trans *ca* 32 maculae; interior plane levis.

Plant Description: *Plants* large, usually about 33cm but up to 1m tall; new growth bright green colour, contrasting with older portions darker to brownish green to black; flexible and resembling *N. flexilis* in the field; *without mucus* (Figs 11-12). *Axes* moderately stout to stout in basal internodes, 600-1250μ in diameter, not encrusted; internodes about equalling upper branchlets in length to about twice the length of lower branchlets, 6-12cm long. *Branches* 1 large branch per node together with 1-2 later-formed and apparently secondary, smaller branches from its base; also usually an adventitious branch at the first furcation of a few or all sterile branchlets per whorl and in lower whorls of fertile branchlets. *Sterile branchlets* 6, 2-3 furcate, up to 8-11cm long, strongly ascending at the upper nodes to a little divergent below (Fig. 7). *Primary rays* about 0.3 to less than half the branchlet length, 2.5-4cm long. *Secondary rays* 2-4, one abaxial, slightly broader and often monopodial or nearly so, some remain simple; and adventitious branch at first furcation often. *Tertiaries* 2-3, divergent but abaxial one less so and nearly or quite monopodial, some remain simple, as long dactyls. *Quaternaries* 2-3, usually as brachydactyls; one may be monopodial and longer, the other shorter and lateral, divergent. *Dactyls* 2-3, (1-)2-4-celled, variable in length, usually very long (2-3cm) as secondaries, or shorter (1cm) as tertiary rays, but brachydactylous (.2-.5mm long) as quaternaries (Fig. 5). A typical long dactyl with a long allantoid basal cell abruptly narrowing to a node, a shorter and narrower second cell also abruptly narrowing to a node, a short, conical, mucronate apical cell, or sometimes two cells in the mucro with the penultimate cell longer or shorter and either tapering smoothly into the end cell or the end cell abruptly mucronate. End cell 55-100μ long, 25-40μ broad at base, (1-celled dactyl: 80μ long, 25μ broad), often deciduous but leaving a truncate scar. *Longer dactyls* appear to result from a failure to fork at an upper node. *Brachydactyls* 2-3, (1-)2-3(-4)-celled, sometimes forming a mucronate 2-3-celled endpiece, smoothly or abruptly tapering down to an acute conical end cell, end cells similar to those on longer dactyls.

Fertile branchlets: (Figs 6, 8, 9), male and female gametangia on separate plants in terminal inflorescences consisting of whorls of 6 branchlets at first compacted into closer heads above, later elongating, spreading and widely spaced below (internodes 2.5-8cm) together with fertile axillary branches. The first fruiting appears at the base of an inflorescence with the development of a fertile axillary branch in a whorl of sterile or nearly sterile branchlets. Later there may be a second, smaller branch. A fertile adventitious branch may appear at the first furcation of the otherwise sterile branchlets in the basal whorl(s). Upwards in the inflorescence second and third branchlet whorls become progressively more fertile, shorter and accompanied by conspicuous fertile axillary branches. These are followed by several (3-4) whorls of completely fertile branchlets which may or may not terminate the stem. It appears in some cases that the growth of the stem axis continues with the production of further whorls of sterile branchlets above the fertile head.

Female inflorescence: lower branchlet whorls 6, 2-3-furcate, from 3-5.5cm long, primary rays 2-2.5cm long, mostly sterile but with fertile axillary branches and occasional adventitious branches at the first branchlet furcation; *upper branchlet whorls* 6, 2-3(-4)-furcate, form 2-2.5cm long; *primary rays* 1-1.5cm long; secondaries 3-4, one secondary ray usually broader, less divergent to monopodial; tertiaries 3-4, one may be central; quaternaries 2-3, one may be central and longer; quinaries 2-3, 2-3-celled, tiny, one ray may be longer. Dactyls 2-4, 2-3-celled, 0.3-4mm long in expanded mature branchlets, end cell short conical, mucronate, 50-120μ long, 25-35μ broad, or a 2-celled terminal mucro, occasionally deciduous.

Oogonia: (Fig. 2), short-stalked, solitary; 675μ (excl. coronula) long, 515μ broad; convolutions 7-8; *coronula* 35μ high, 50-55μ broad at base, upper cells overarching, 2-3 times longer than lower.

Oospores: (Fig. 1), dark, chestnut brown, 515μ long, 325μ broad; striae of 5 prominent and flanged ridges; fossa 80μ across; *membranes*: (Figs 3-4), outer, densely granulate to vermiferous; middle, finely reticulate about 32 meshes across; inner, smooth and clear.

Male inflorescence: lower branchlet whorls 6, 2-3-furcate, about 3-5cm long, similar to the female in arrangement, composition, and fertility but somewhat more spreading to reflexed, somewhat protandrous. *Primaries* about half the branchlet length, *secondaries* 3-4, *tertiaries* 2-4, *quaternaries* 2-3 where present, *quinaries* 2-3, 2-celled dactyls here present. *Dactyls:* 2-3, (1-)2-3-celled, up to 1.5cm long, or brachydactylous and (1-)2-3 very short cells in length. *Upper branchlet whorls* 6, 2-3(-4)-furcate, closer, shorter and more fertile than the branchlets below as in the female.

Antheridia: solitary at 2nd, 3rd and 4th furcations, absent at the first branchlet node, sometimes terminal at end of tertiary ray or 8 accompanied by minute quaternary dactyls; 450μ long, 420μ broad, 8-scutate.

Chromosomes: A chromosome number of n = 9 was established for *Nitella woodii* (A. and D. Hotchkiss) unpublished.

Turions: Muenscher (1944) calls a turion 'a hardened abbreviated axis or winter bud as in *Potamogeton*'. The use of the term 'turion' herein comes from a combination of suggested morphological and physiological similarity.

Winterbud-like structures or turions were observed from March to July on sterile overwintering plants in the Nepean River (Figs 10, 11, 13). The turions consisted of greatly swollen, starch-filled, food-storage cells. Turions in a main stem axis might include a single condensed whorl of primary rays, or primaries, secondaries and sometimes tertiaries as well, or two successive branchlet whorls including the connecting internodal cell. Often, a short axillary branch including the stem axis and one of two whorls of branchlets forms an axillary turion. The swollen ray cells form long narrow cylinders gradually tapered at the base, but abruptly tapered at the apex, and all become quite rigid.

Turions were brought into the laboratory and cultured in pans of water under lights in a constant temperature room. Germination was first observed in June after 4 to 6 weeks of cultivation. New growth from the turions produced normal stems and branchlets.

Occasionally in sterile branchlet whorls, more rarely in fertile whorls, new turions appear in the upper shoots with the new growth of early spring (August) and production of turions continues through the fruiting season (October-November). At this time it was seen that young turions may be fertile on normal nodes at a few furcations above the swollen turion rays. An attempt to germinate new turions was unsuccessful through December when the experiment was terminated.

Turion cells appear to be longer-lived and more resistant to adverse conditions than are the ordinary vegetative cells in both culture and in the field where they often become detached as a group and survive when other nearby cells are dead. It is likely that detached turions can serve as propagules and disseminules for the species. It seems possible that young turions possess some degree of dormancy which may assist in this role.

Turions such as these are apparently a useful taxonomic tool for delimiting *Nitella woodii* from many charophytes. They are probably not restricted to this species. For example, the second author found 'turions' in Japanese specimens of *Nitella annularis*. In addition, Wood and Imahori (1965) provided illustrations of *Nitella tumida* and *Chara submollusca*, which strongly suggest the presence of turions in the enlarged, inflated primary rays in certain whorls of branchlets.

RELATIONSHIPS

The establishment of this member of the genus *Nitella* as a new species was the result of a series of studies and observations.

(1) This large, robust species, complete with its unusual turions, was unique among all previously-studied forms.

(2) The differences in morphology coupled with its seasonal maturation in late winter, early spring, distinguished it from other charophytes in the Nepean River area.

(3) In its strong tendency to monopodial branchlet axis rays, the new species might be considered close to the *Nitella cristata* complex, (Wood and Imahori, 1965). It is

easily separated from *N. cristata* by additional morphological characteristics and by its difference, locally, in maturation time.

(4) As in much of the genus *Nitella*, the relationships of this species are most clearly indicated by the nature and number of cells in the dactyls. Its 1-4-celled dactyls place the species in the pluricellulate series of the Arthrodactylae. A combination of morphological characters narrows it down within the confines of Wood's key (1965) to the Section Incertae which contains *Nitella hookeri*, tentatively assigned as a form of the subgenus *Nitella* (which also includes *Nitella flexilis*) and *Nitella tasmanica*, in the subgenus *Hyella*.

The species resembles dioecious *N. tasmanica*, somewhat, but in general habit and in the form of its dactyls, it is closer to the monoecious *N. hookeri*. The two may be separated by *N. hookeri*'s geminate oogonia and coarsely reticulated oospore membrane. A chromosome number of n = 18 (A. and D. Hotchkiss, unpublished) was established for the monoecious *N. hookeri* (sensu *N. tricellularis*, fide R. D. Wood, collected by Wood in New Zealand) in 1961, whereas the dioecious *Nitella woodii* has a chromosome number of n = 9.

It would appear that the morphology of the species, its dioecious condition and its chromosome number provide sufficient distinctions to establish *Nitella woodii* as a separate species.

The new species has been named *Nitella woodii* in honour of the late Professor R. D. Wood, a leading student of the Charophyta.

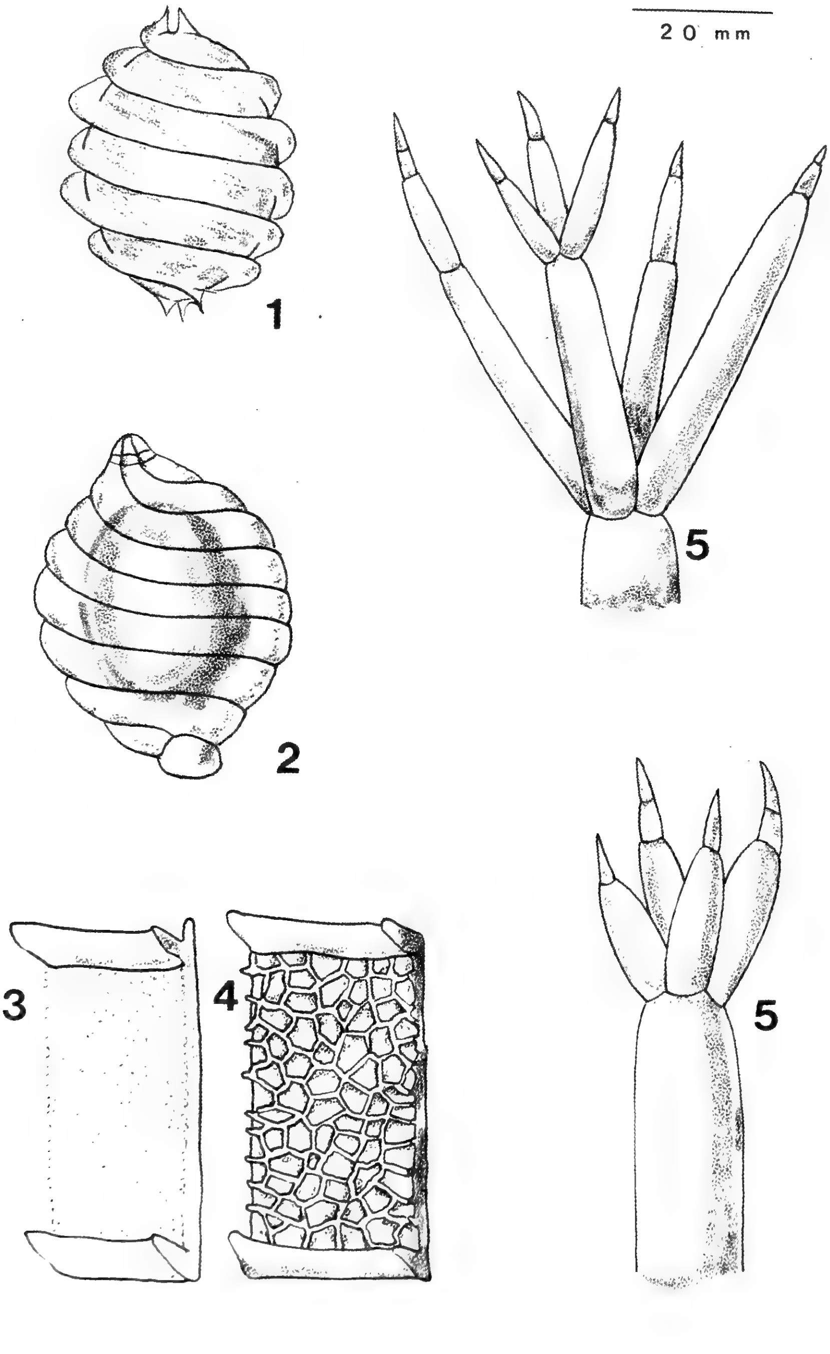
ACKNOWLEDGEMENTS

We wish to express our deepest appreciation for the interest shown and the help extended in collection and preservation of materials by the late John Waterhouse of the University of New South Wales.

References

MUENSCHER, W. D., 1944. — Aquatic Plants of the United States. (x + 374). Ithaca, N.Y.: Comstock Pub. Co.

WOOD, R. D., and IMAHORI, K., 1965. — A Revision of the Characeae. Vol. 1. *Monograph of the Characeae* (by R. D. WOOD, illustrated by K. IMAHORI). (xxiv + 904). Weinheim, Germany: J. Cramer



Figs 1-5. 1, Oospore, x90. 2, Oogonium, x75. 3, Spore Membrane, lower focus, x600. 4, Spore Membrane, higher focus, x600. 5, Dactyls at apices of sterile branchlets, x75.

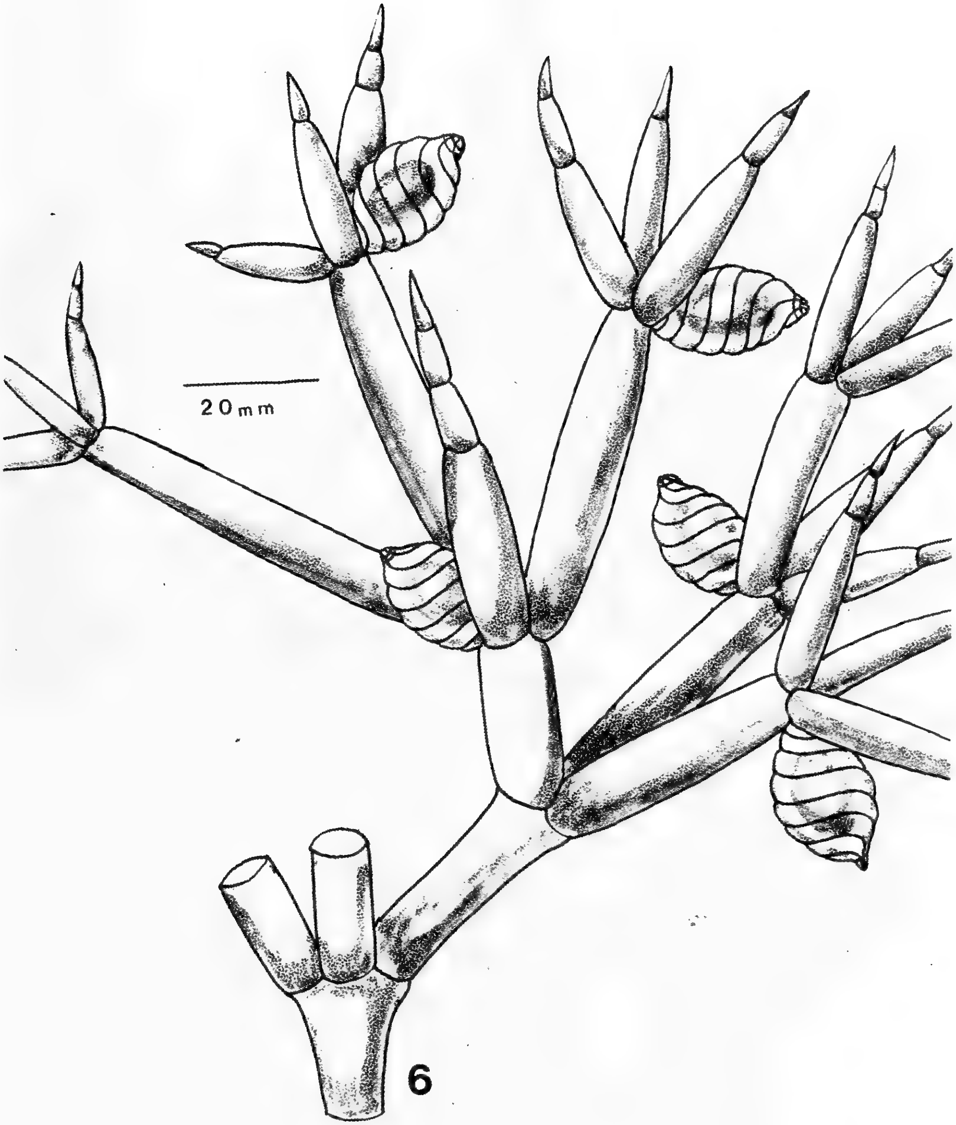
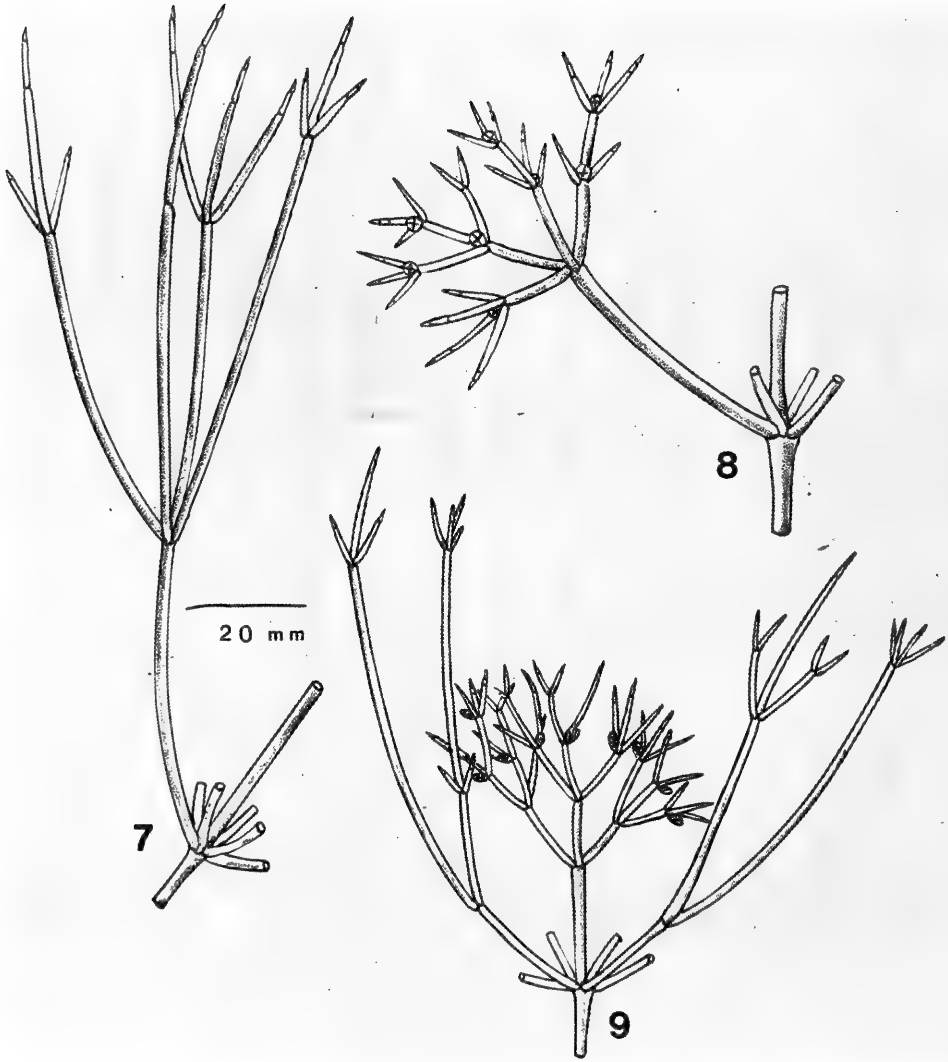


Fig. 6. Fertile female branchlet, x30.



Figs 7-9. 7, Sterile branchlet, x4.5. 8, Male branchlet, x9. 9, Female branchlet, x6.

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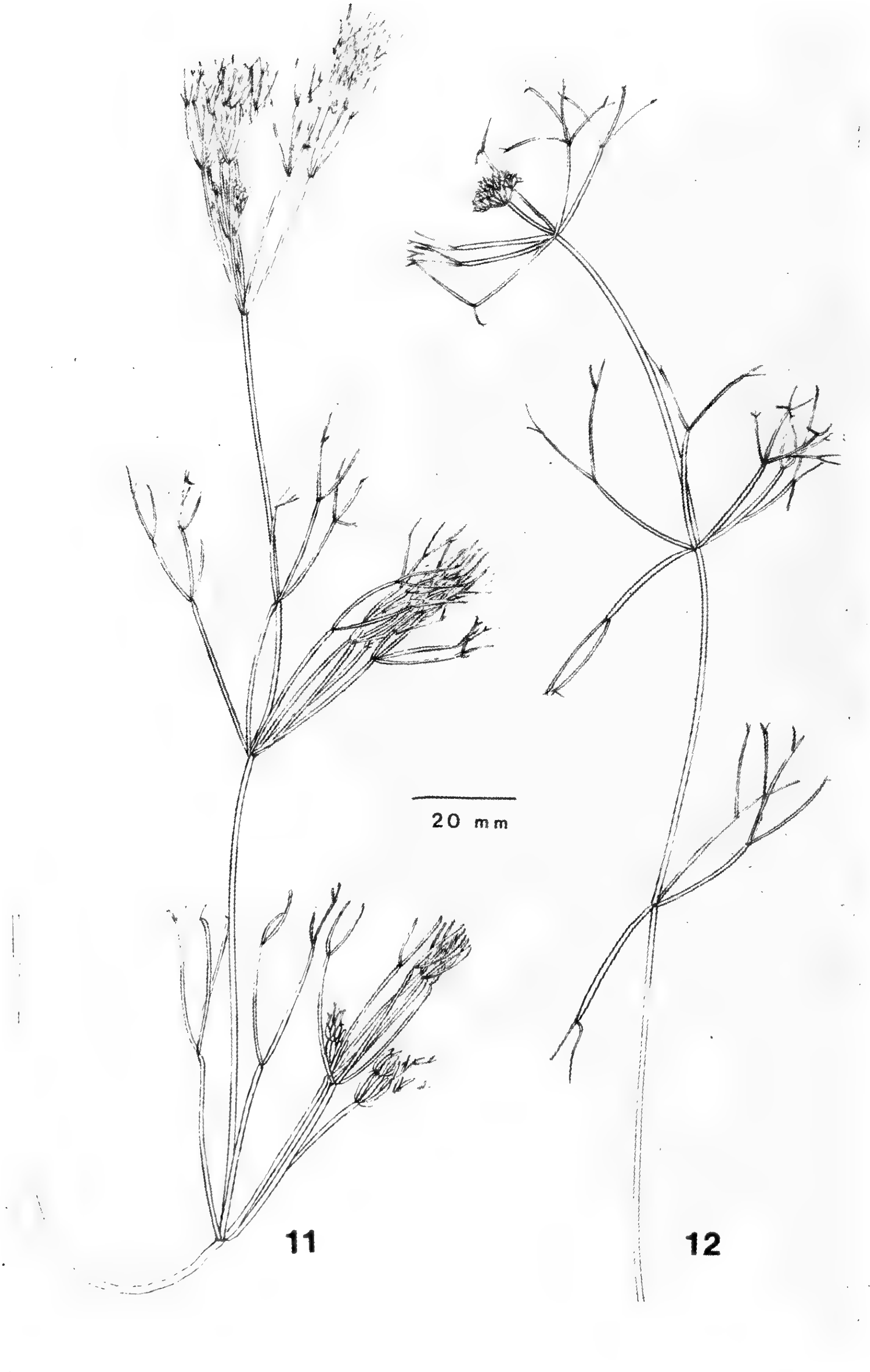
Fig. 10. Turions in two whorls of branchlets, x7.5.



Figs 11-12. 11, Habit of female plant, turions in lower branchlet whorl, x3/2. 12, Habit of male plant, x3/2.

Fig. 13. Turions stained with iodine. Slide prepared and photographed at the University of Sydney.

Additional Observations on *Nitella verticillata* (Characeae) from a new Locality in New South Wales*

A. T. HOTCHKISS and K. IMAHORI

HOTCHKISS, A. T., & IMAHORI, K. Additional observations on *Nitella verticillata* (Characeae) from a new locality in New South Wales. *Proc. Linn. Soc. N.S.W.* 110 (2), (1987) 1988: 187-191.

Abundant fertile material of dioecious *Nitella verticillata* (with mucus) from brackish coastal lagoon Lake Munmorah, New South Wales, permits description of monopodial male plants, antheridia, oogonia and spores, in a species heretofore known only from limited material in Western Australia, South Australia and Victoria.

A. T. Hotchkiss, Professor Emeritus, Department of Biology, University of Louisville, Louisville, Kentucky, 40292, U.S.A., and K. Imahori, Vice-President, Naruto University of Teacher Education, Takashima, Naruto-Shi, 772, Japan; *manuscript received 17 September 1986, accepted for publication 19 August 1987.*

INTRODUCTION

Nitella verticillata was first collected by Nancy Burbidge (1956, 1960), from Lake Parkeyerring, a shallow salt water lake near Wagin, Western Australia, June 5, 1933. The specimens she sent to G. O. Allen in England proved to be sterile, incomplete, and scanty.

Allen sent the material to Filarszky (1937) in Hungary, who in turn described it and set it up as a monotypic genus, *Charina*, and established *Charina verticillata.* Although no gametangia were available the new species was designated monoecious.

Wood and Imahori (1964, 1965) further described and illustrated the species from the incomplete sterile specimens available from G. O. Allen, and added some details. The species was transferred at this time to the genus *Nitella* by Wood.

Wood (1972) reported finding the species in two new localities: Lake Bunijon, Victoria, and the Thorndon Park Reservoir near Adelaide, South Australia. He pointed out that the material was 'so small and threadlike' that during the course of a year collecting in Australia, he did not detect it in the field, but found it only because fragments were entangled with plants of other Characeae collected in Victoria and South Australia. The material yielded female gametangia and oospores which he described and led him to suggest that the species might be dioecious rather that monoecious. He summarized the habitat of the species in the three Australian States as follows: 'shallow water of flooded field or lake; firm bottom; fresh water, possibly tolerant of at least slight salinity'. Finally, Wood separated the new material in his key on the basis of its bicellulate dactyls, its monopodial branchlets and its small size.

In February, 1976, the first author collected *Nitella verticillata* at Lake Munmorah, north of Sydney, New South Wales. Lake Munmorah is a coastal lagoon lake with an inlet to the sea opening between sand dunes along the coast. Salinity varies with the rainfall. At the time of collecting, after an unusually rainy season with high water, the salinity level was reported to be 12.3 p.p.m. In time of drought, this varies up to 18 p.p.m. The species was found growing with *Lamprothamnium* and *Chara* species. *Nitella verticillata*

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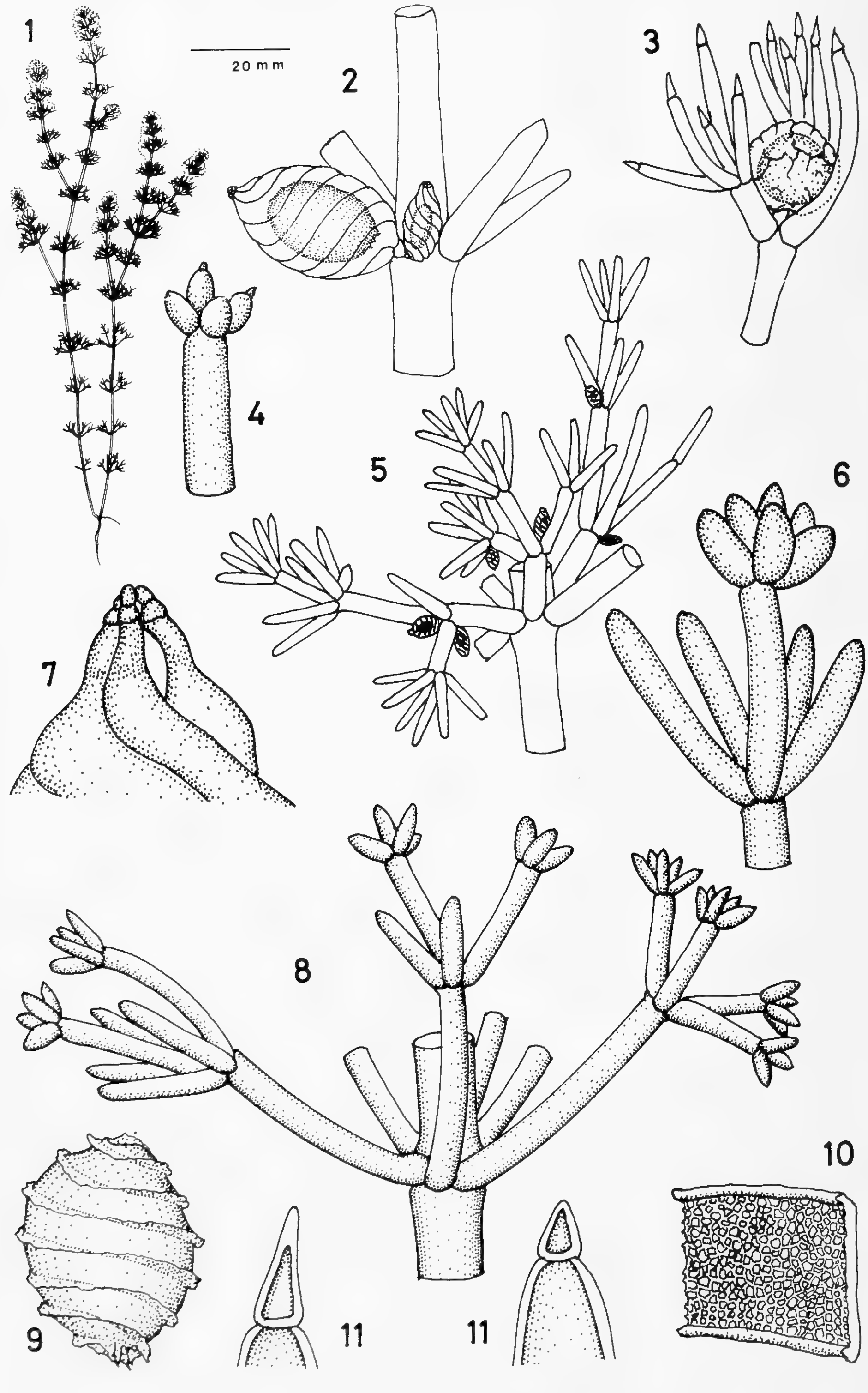
* A paper presented at the International Seaweed Symposium, Santa Barbara, California, U.S.A., August 1977.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was growing on the flooded sandy, pebbly beaches with *Lamprothamnium* and *Chara* in deeper water nearby.

Observations

Collections: Lake Munmorah near Ashdam Creek and power plant inlet canal. A. T. Hotchkiss 76-2-24-1. Drawings made by K. Imahori, Figs 1-14.

Description: *Nitella verticillata* (Fil. et G. O. Allen ex Fil.) R. D. Wood

Plants dioecious, male and female plants similar vegetatively, bright to dark green, much branched and growing together, up to 8cm high, (Fig. 1). Axis moderately slender to 330μ in diameter: internodes as long as fertile whorl, 2-3 times as long as sterile branchlets.

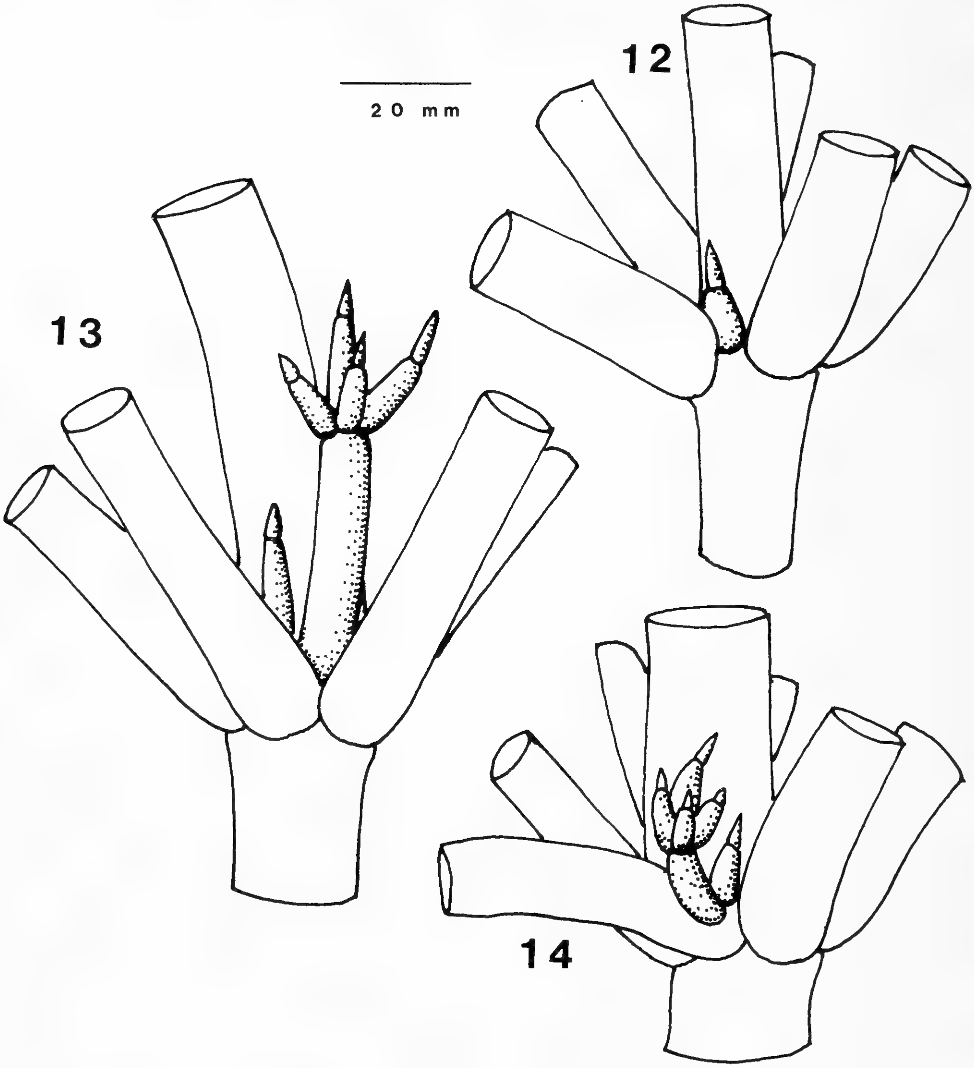
Branchlets 6-8 in a whorl, 1-3 furcated, (Fig. 5). Fertile branchlets covered with mucus and commonly congested into heads to 2mm long; primary rays ⅓ to ¼ of the entire length; secondary rays 3-4, of which 1 is usually the central ray, but absent when an oogonium or antheridium is produced terminally, and 1-3 lateral rays being dactyls usually; tertiary rays 4-6 (very rarely only 1) of which central and some lateral rays furcate once more into 4-6 terminals. Branchlet nodes on male plants commonly whorls of six lateral rays plus short central axis terminating in an antheridium which is solitary and octoscutate. Sterile branchlets somewhat diffuse (Fig. 8), 1-2 times furcated; primary rays $^2/_3$ to $^3/_5$ of the entire length; secondary rays 4-6 of which 1 is occasionally central; tertiary rays 3-4. Dactyls (Figs 4, 6), elongated on fertile branchlets and at the primary node of the sterile branchlets; abbreviated and percurrent usually at the primary node of the sterile branchlets, abbreviated and percurrent usually at the second node of fertile branchlets; uniformly 2-celled but seems unicellular because of the deciduous end cells, (Fig. 6); end cells acute or acuminate, 39-100μ wide at the base (Fig. 11).

Occasionally 1 to 4 dwarf branchlets or accessories produced at the base of sterile whorls, (Figs 12-14), 200 to 600μ long; branchlets simple (as a single dactyl) or once furcated into 3-4 dactyls.

Gametangia produced at the 1st and 2nd nodes of branchlets. Oogonia solitary or geminate, (Fig. 2), terminal or laterally produced; 550 to 580μ long (including the coronula) and 375 to 400μ wide; spiral convolutions 8-9; swollen at the base of coronula, (Fig. 7). Coronula small, 35-40μ high, 60 to 65μ wide at the base. Oospores bright to dark brown (Fig. 9); subglobose and compressed, 320 to 350μ long, 280 to 300μ wide and 180 to 200μ thick; striae prominent and flanged, 6-7; fossa 50 to 55μ; membranes (Fig. 10), bright brown, finely reticulated; 12 to 14 meshes across fossa, arranged in a line series. Antheridia (Fig. 3), solitary and terminal; stalk cell 30 to 60μ long by 30μ diameter; antheridia 250 to 330μ diameter.

Chromosome number, n = 9.

Figs 1-11. 1, Plant habit, with mucus around heads, natural size. 2, Geminate, lateral oogonia, with secondary rays surrounding central monopodial, secondary ray, x35. 3, Solitary antheridium, terminal on short, central, secondary ray, x35. 4, Short, ovoid dactyls, x35. 5, Part of a female plant showing whorl of branchlets, x15. 6, Dactyls from which the end cells have fallen off, x35. 7, Apex of oogonium, somewhat swollen at the base of coronula, x150. 8, Part of a sterile whorl of 6 branchlets, x150. 9, Oospore, with 6-7 prominent and flanged striae, x65. 10, Oospore membrane, finely reticulated, 12 to 14 meshes across fossa arranged in a somewhat linear series, x270. 11, End cells of dactyls mucronate, acute or acuminate, often deciduous, x150. (Linear scale for Figs 1-11 is 20 mm.)



Figs 12-14. Dwarf accessory branchlets, x35. 12, Non-furcating branchlet. 13, Non-furcating and once furcated branchlets. 14, Two dwarf branchlets produced between central and lateral rays. (Linear scale for Figs 12-14 is 20 mm.)

RELATIONSHIPS

Wood (1964, in Wood and Imahori, 1964), without benefit of gametangia, placed *Nitella verticillata* in his subgenus *Tieffallenia*, Section 8, Migularia with three other species, *Nitella struthioptila*, *N. imahorii* and *N. cristata*. The positioning was based strictly on the arrangement of the percurrent central branchlet ray, a type of branchlet found in a few other species including the *N. cristata* complex. The small *N. verticillata* with its 1-2 cell dactyls is easily separated from the larger *N. cristata* with its 3-4 cell dactyls.

A new species described by Williams (1959), *Nitella reticulata* from a coastal sand dune pond near Sydney, with its reticulate spore membrane and brackish water habitat, is suggestive of *N. verticillata* but its dactyls, furcation and size serve to separate it from *N. verticillata*.

The *Nitella hyalina* species group, in the same subgenus *Tieffallenia*, but in Section 4, Decandollea, is often found in saline water or near coastal areas. The group has strongly percurrent branchlet axes and an abundance of mucus. However, its well-developed accessory branchlets and its much larger size separate it easily from *N. verticillata*.

The additional material provides an opportunity for further study of the position of the relatively obscure *Nitella verticillata* within the genus *Nitella* and of the importance of several key characteristics, such as the percurrent central branchlet ray. More extensive data on oogonial structure and the oospore membrane will fix its relationships more fully. In additon, the new details on antheridial structure and the arrangement of the male branchlets, enables this species to be subject to as critical analysis and comparison as any of the best known members of the Characeae.

References

BURBIDGE, N. T., 1956. — Robert Brown's Australian collecting localities. *Proc. Linn. Soc. N.S.W.* 80: 229-233.

——, 1960. — The phytogeography of the Australian region. *Aust. J. Bot.* 8: 75-212.

FILARSKY, N., 1937. — Idigenföldi Charafélék határozása. (Determinatio Characearum exoticarum). *Magyar Tud. Akad. Mat. Term. Ert.* 55: 476-497, 6 pl. incl. 46 fig.

WILLIAMS, M. B., 1959. — A revision of *Nitella cristata* Braun (Characeae) and its allies. Part II. Taxonomy. *Proc. Linn. Soc. N.S.W.* 84: 346-356.

WOOD, R. D., 1972. — Characeae of Australia. *Nova Hedwigia* 22,ii:1-120.

——, and IMAHORI, K., 1964. — Vol. 2. *Iconograph of the Characeae. A Revison of the Characeae.* Weinheim: Cramer.

——, and ——, 1965. — Vol. 1. *Monograph of the Characeae. A Revision of the Characeae.* Weinheim: Cramer.

A new Australian larval Callidosomatine Mite (Acarina: Erythraeidae) parasitic on Flies, with Notes on Subfamily and Tribe Classification

R. V. SOUTHCOTT

SOUTHCOTT, R. V. A new Australian larval callidosomatine mite (Acarina: Erythraeidae) parasitic on flies, with notes on subfamily and tribe classification. *Proc. Linn. Soc. N.S.W.* 110 (2), (1987) 1988: 193-204.

A larval mite *Carastrum ferrari* n. gen., n. sp. (Acarina: Erythraeidae: Callidosomatinae: Callidosomatini), parasitic on Diptera is described from New South Wales. The larvae, generally one per fly, select the ventral surface of the host fly for attachment, in most cases the metasternal-abdominal tergite I membrane.

A revised key to the genera of larval Callidosomatini is given, and formal definitions of the tribal names Callidosomatini and Charletoniini.

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INTRODUCTION

The subfamily Callidosomatinae was introduced by Southcott (1957), and later (Southcott, 1961b) divided into the tribes Callidosomatini and Charletoniini, in keys, but hitherto without formal text definitions for the tribes.

Southcott (1972) left the Callidosomatini with three genera known as larvae: *Caeculisoma* Berlese, 1888, *Callidosoma* Womersley, 1936 and *Momorangia* Southcott, 1972. In this paper a further genus of Callidosomatini is described, from larvae captured ectoparasitic on flies in New South Wales, *Carastrum ferrari* n. gen., n. sp.

Abbreviations for scutal dimensions are as in Southcott (1966, 1972), and for leg segmental dimensions as in Southcott (1986). Seta coding terminology follows Southcott (1961b,c, 1966, 1972).

All measurements are in micrometres (μm) unless otherwise indicated.

SYSTEMATICS

Tribe CALLIDOSOMATINI Southcott

Callidosominae Southcott, 1957, p. 97.
Callidosomatinae Southcott, 1961b, p. 521.
Callidosomini Southcott, 1961b, p. 522.
Callidosomatini Southcott, 1972, p. 1.

Diagnosis

Adults: Callidosomatinae with usually distal tubercles on pedal tibiae.

Larvae: Callidosomatinae with scutalae 3+3 or more. Pedocoxalae 1, 2, 2. Pedotrochanteralae 1, 1, 1. Posterior pedotibial claw hooklike. Palpal tibial claw (odontus) without accessory peg or basal process.

Type genus *Callidosoma* Womersley, 1936.

Comment: The tribe Callidosomatini was based primarily on the characters of the adults (and deutonymphs), these being generally mites with short, thick legs with prominent distal tubercles.

Since then Sharma, Farrier and Drooz (1983) have described the adult and deutonymphal instars of *Callidosoma metzi* Sharma, Drooz and Treat, 1983 from North

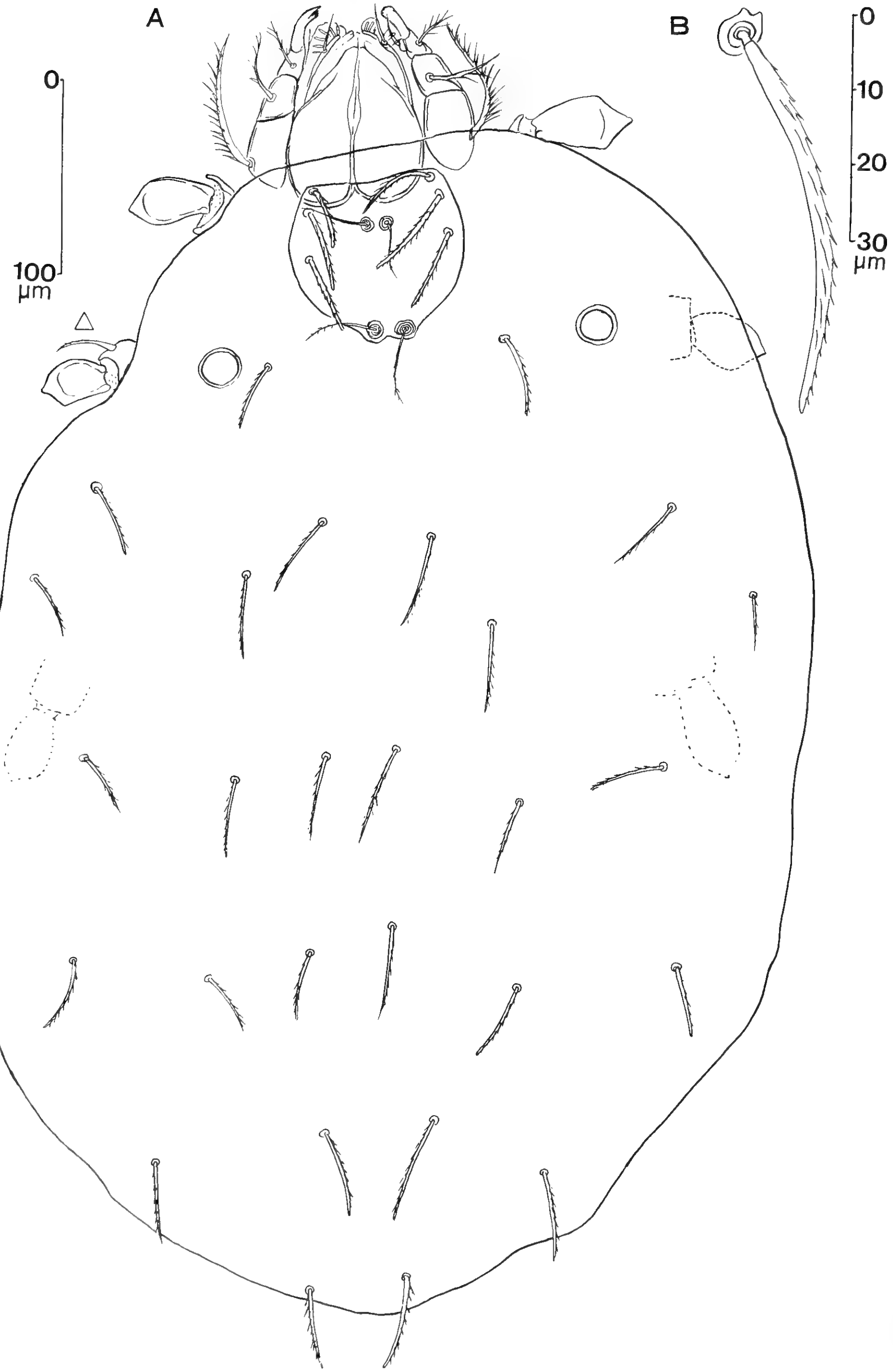

Fig. 1. Carastrum ferrari n. gen., n. sp. **A**, Dorsal view of Holotype larva, partly in transparency, with legs omitted beyond trochanters. **B**, Dorsal idiosomal seta ('ocular'), from Paratype ACA1892B. (Both figures to nearer scale.)

and Central America, and record (both papers) that tibial tubercles are lacking in both of these instars. The larva, however, answers to the criteria of *Callidosoma* of Southcott (1972). Treat (1985) has recorded that the deutonymphs of *Callidosoma apollo* Southcott from North America also lack tibial tubercles. He pointed out various overlaps of the characteristics of the larvae of *Callidosoma* and *Caeculisoma*, and stated that there are thus unresolved problems in the classification of 'generic or tribal taxa'.

See also the comment after the definition of Charletoniini, below.

Key to genera of larval Callidosomatini

1. Scutalae 4 + 4 or more . . . . *Momorangia* Southcott
   Scutalae 3 + 3 2
2. Palpal tibial claw with 4-5 terminal teeth . . . . *Carastrum* n. gen.
   Palpal tibial claw with two prongs 3
3. Anterior scutal sensilla not posterior to level of ML scutalae . . . . . . *Callidosoma* Womersley
   Anterior scutal sensilla posterior to level of ML scutalae . . *Caeculisoma* Berlese.

Carastrum n. gen.

Etymology: The name *Carastrum* is derived from the *Ca-* of Callidosomatini, and Latin *rastrum*, a rake, referring to the structure of the palpal tibial claw.

Diagnosis (based upon larval characters): Callidosomatini with scutalae 3 + 3. Palpal tibial claw with 4-5 terminal teeth. All tarsal claws hooklike, the posterior with three large ventral setules. Pedotibia II with a large solenoidala.

Type species *Carastrum ferrari* n. sp.

Carastrum ferrari n. sp.

Figs 1 **A,B,** 2**A-C**, 3, 4**A-H**, 5, 6

Etymology: The specific name is in honour of the collector.

Material examined (larvae only; adults and deutonymphs not known): **Holotype** with label ACA1892G2, parasitic on fly A2808, 2 miles [3.2 km] W of Durras (north of Batemans Bay), New South Wales, 14.ii.1972, P. Ferrar.

Paratypes: Nine other specimens, same locality, date and collector, on flies *Pyrellia tasmaniae* Macquart, *Helina* sp., and undetermined calyptrates. Mites labelled ACA1892A-F, G1, H1, H2, on flies A2802-8, 2809, 2809 respectively.

All mites deposited in South Australian Museum collection; host Diptera in Australian National Insect Collection, Canberra.

Description of Holotype (supplemented by paratypes): Colour red. Ovoid, flattened below, with some grooves of idiosoma extending to lateral outlines. Length of idiosoma in ethanol 585, width 415, overall length including mouthparts 640; after mounting through lactic acid-Hoyer's medium length 610, width 440, overall length 675.

Dorsal scutum rounded, with shallow concave anterior margin, convex lateral margins except immediately before the protrusions for the posterior sensilla, with a notch between. Anterolateral angles rounded. Scutalae normal, curved, tapering, slightly blunted, with strong setules; AL at AL angles of shield, ML a little behind and lateral to them, PL further lateral but anterior to mid-level of shield. Scutal sensillary setae filiform, tapering, with a few distal setules.

TABLE 1

Standard Data of three specimens of Carastrum ferrari

	ACA1892G2 Holotype	ACA1892A Paratype	ACA1892B Paratype
AW	61	59	57
MW	66	69	66
PW	71	73	71
SBa	11	10	9
SBp	15	14	14
ASBa	23	25	26
ISD	55	55	56
L	85	86	89
W	80	90	88
A-M	11	14	15
A-P	31	35	35
AL	55	49	58
ML	55	58	55
PL	52	47	48
ASens	45	45	42
PSens	69	66	67
ASBa/ISD	0.42	0.45	0.46
DS	46-53	45-49	46-55
Oc.	46	—	47
MDS	46	45	55
PDS	53	49	46
GeI	91	87	87
TiI	109	112	112
TaI(L)	98	113	109
TaI(H)	19	19	19
GeII	80	77	82
TiII	93	102	108
TaII(L)	107	104	107
TaII(H)	19	18	19
GeIII	83	82	87
TiIII	160	155	157
TaIII(L)	115	114	120
TaIII(H)	19	17	17

The Standard Data of the Holotype and two Paratypes are as in Table 1.

Eyes 1+1, posterolateral to scutum, corneae circular, width 18.

Dorsum of idiosoma with 28 setae, curved, slightly tapering, blunt-pointed, with strong setules; arranged 2 (oculars), 4, 4, 6, 6, 4, 2.

Venter: sternalae I robust, tapering, pointed, well setulose, 45 long; sternalae II similar, 53; sternalae III similar, 53. Behind coxae III 14 similar setae, arranged 4, 4, 4, 2; 29-45 long, the more posterior shorter and tending to resemble posterior dorsal idiosomalae.

Coxalae 1, 2, 2; coxala I tapering, pointed, well setulose, 76; lateral coxala II similar, 48, medial coxala II similar, 75; lateral coxala III similar, 50; medial coxala III similar, 60.

Legs of normal callidosomatine build. Specialized setae (from ACA1892B): Genu I with SoGeI.81d(20 long), VsGeI.87pd(5). Tibia I with Cp.61d(6) + SoTiI.62d(20) ('duplex pair'), SoTiI.69d(27), VsTiI.84pd(5). (Most distal seta of tibia I is ScTiI.83v(22)). Tarsus I with SoTaI.35d(27), SoFaI.51d(2). Genu II with VsGeII.87pd(5). Tibia II with SoTiII.09d(31). Tarsus II with SoTaII.45d(24). Tibia III with greatly enlarged solenoidala SoTiIII.04d(66). Pretarsal formula 1, 1, 1.

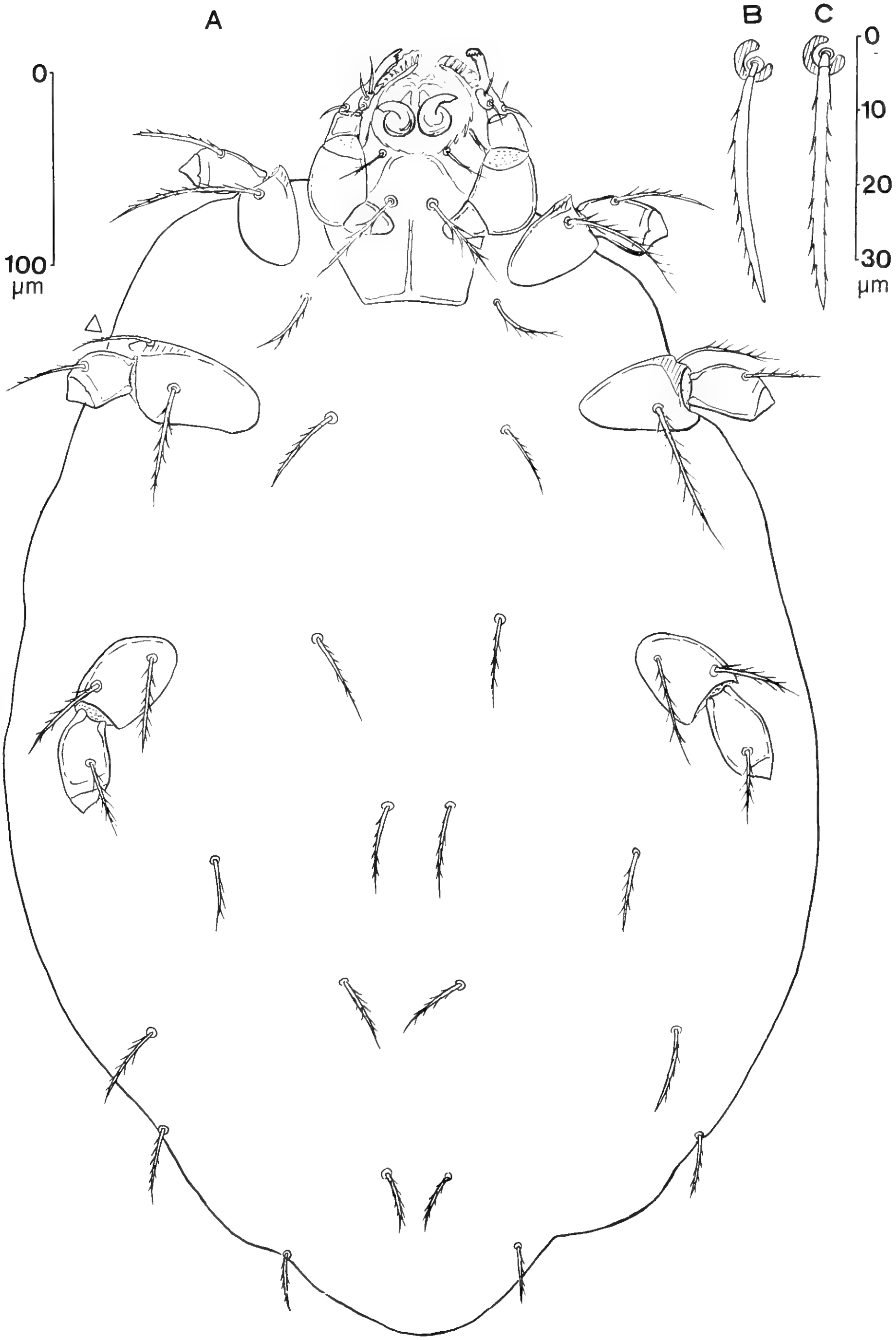

Fig. 2. Carastrum ferrari n. gen., n. sp. **A**, Ventral view of Holotype larva, with legs omitted beyond trochanters. **B, C**, Posterior ventral setae of idiosoma, from Paratype ACA1892B. (All figures to nearest scale.)

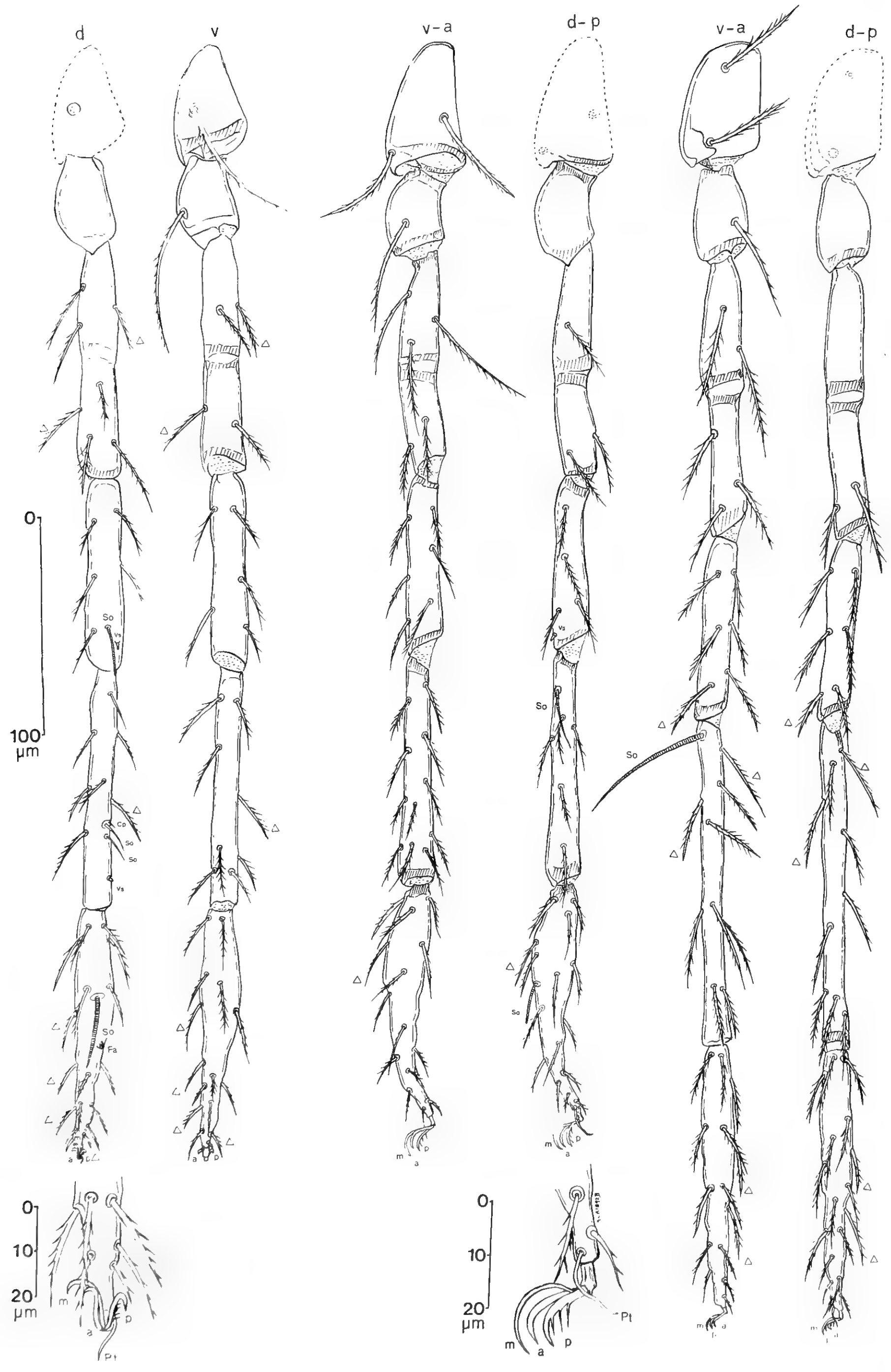

Fig. 3. Carastrum ferrari n. gen., n. sp., larva. Legs I, II, III of Paratype larva ACA1892B, to standard symbols; to scale on left. Inset: Tips of tarsi I and II, to scales alongside: I dorsal aspect, II posterior aspect; Pt pretarsala.

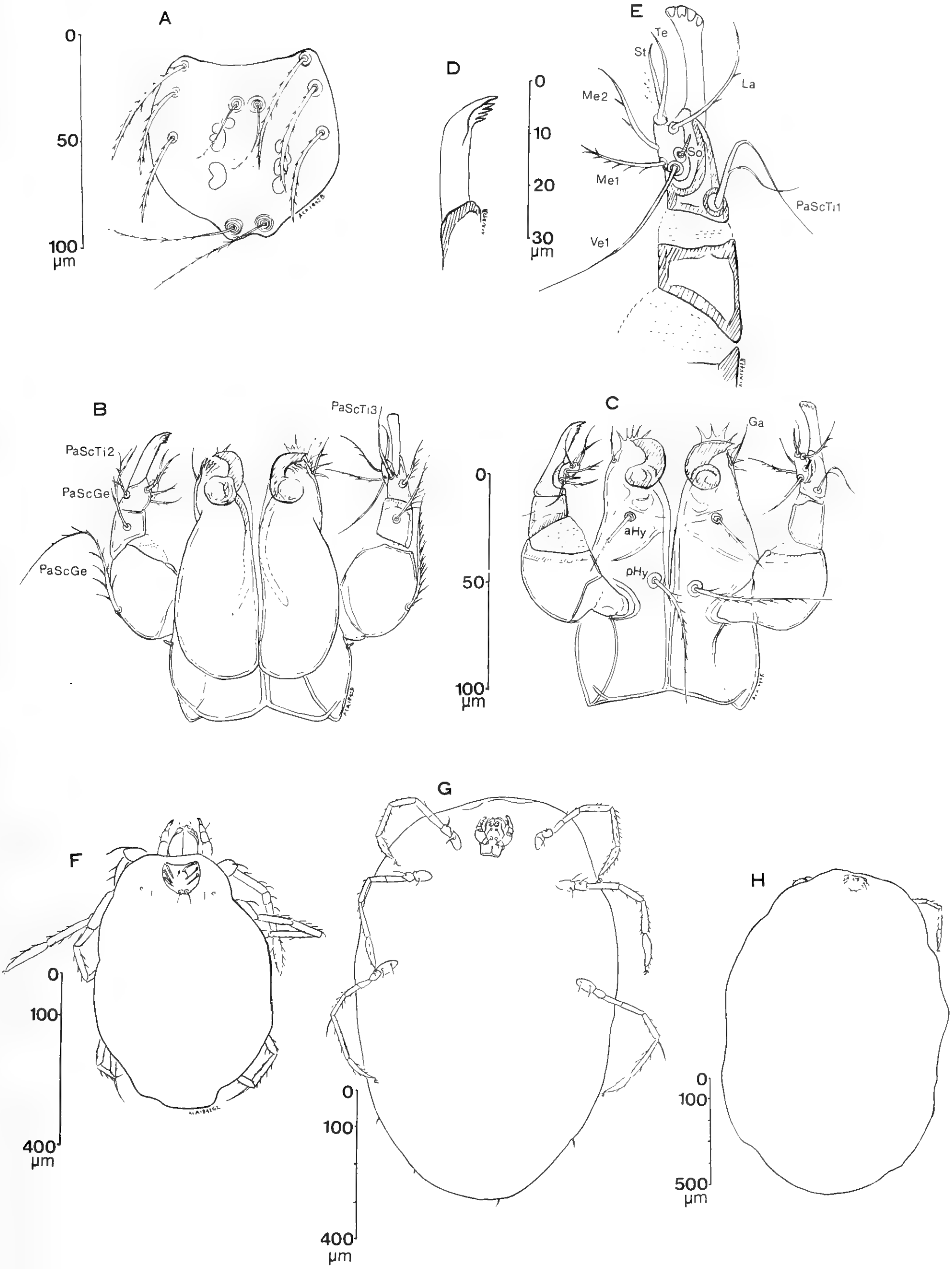

Fig. 4. Carastrum ferrari n. gen., n. sp., Larva. **A**, Dorsal scutum. **B**, Gnathosoma, dorsal view. **C**, Gnathosoma, ventral view. **D**, Palpal tibial claw, medial aspect, in dorsal view (see **B**). **E**, Tip of palp, ventral aspect (see **C**). (**A-E** from Paratype ACA1892B.) **F**, Holotype, dorsal view, in preservative before clearing. **G**, Large specimen, Paratype ACA1892C, after mounting, ventral aspect showing gnathosoma on ventral surface. **H**, Large specimen, dorsal aspect, in preservative, Paratype ACA1892G1, showing dorsal scutum retained in position at anterior pole of idiosoma. (All to nearest scale.)

Gnathosoma robust, chelicerae rounded, width (combined) 71, length 91. Cheliceral fangs curved, with oblique terminal cutting edge. Gnathosomal lip fimbriated. Anterior hypostomala tapering, pointed, well setulose, 24; posterior similar, 66. Galeala slender, pointed, nude, 27.

Palpal setal formula 1, 1, 3, 7. Palpal femorala arises laterally, slender, pointed, setulose, 65; palpal genuala arises dorsally, similar, 40. Other palpal setae as figured. Palpal tibial claw broadened at end, to carry 4-5 small, pointed teeth. Palpal supracoxala a short blunted peg, 6 long.

Remarks on the type series

These larval mites were all partly fed. The smallest available, and hence most suitable for detailed description, was selected as the Holotype. Swelling of the idiosoma due to feeding in larger specimens obscures the characters of the gnathosoma.

Details of the sizes of the larvae (measured in ethanol, except A. B, which are estimated from the slide mounts) and host identifications are given in Table 2.

TABLE 2

Sizes and host Diptera identifications of Carastrum ferrari *n. gen., n. sp.*
H = *Helina* sp.; PT = *Pyrellia tasmaniae* Macquart (Muscidae). MF = unnamed calyptrate.

Mite number ACA1892	Length of mite	Width of mite	Fly number	Fly identification
A	ca 1500	ca 900	A2802	H
B	ca 600	ca 400	A2803	MF
C	990	610	A2804	PT
D	1585	1045	A2805	MF
E	1870	1280	A2806	H
F	1530	1115	A2807	H
G1	1600	1175	A2808	H
G2	585	415	A2808	H
H1	1100	650	A2809	H
H2	845	470	A2809	H

Remarks on biology

All of the mites were attached to the ventral surface of the fly, and all except one to the membrane connecting the metasternum and abdominal tergite I. In the two cases in which two mites attached to the host fly, in one the two mites were attached to the metasternum-abdominal tergite I membrane, and in the other case one mite was on this membrane, and the other on the prosternum. The largest of the larval mites (ACA1892E) equalled in size the abdomen of the host fly (see Fig. 5).

Mites of the tribe Callidosomatini have been recorded as larval ectoparasites of Lepidoptera (Womersley, 1934; Southcott, 1972; Treat, 1975, 1985; Sharma, Drooz and Treat, 1983; Sharma, Farrier and Drooz, 1983), Homoptera (Southcott, 1946, 1972) and Orthoptera (Southcott, 1961a, 1972). Although this is the first Australian record of Diptera being parasitized by members of the Callidosomatini, there is a previous record of one species, *Callidosoma tiki* Southcott, parasitizing an unidentified dipteran in New Zealand (Southcott, 1972), and mites referred to *Callidosoma* spp., but not further determined, have been recorded from Culicidae in North and Central America by Mullen (1975), Welbourn (1983) and Treat (1985), and from Trichoptera in North America by Resh and Haag (1974).

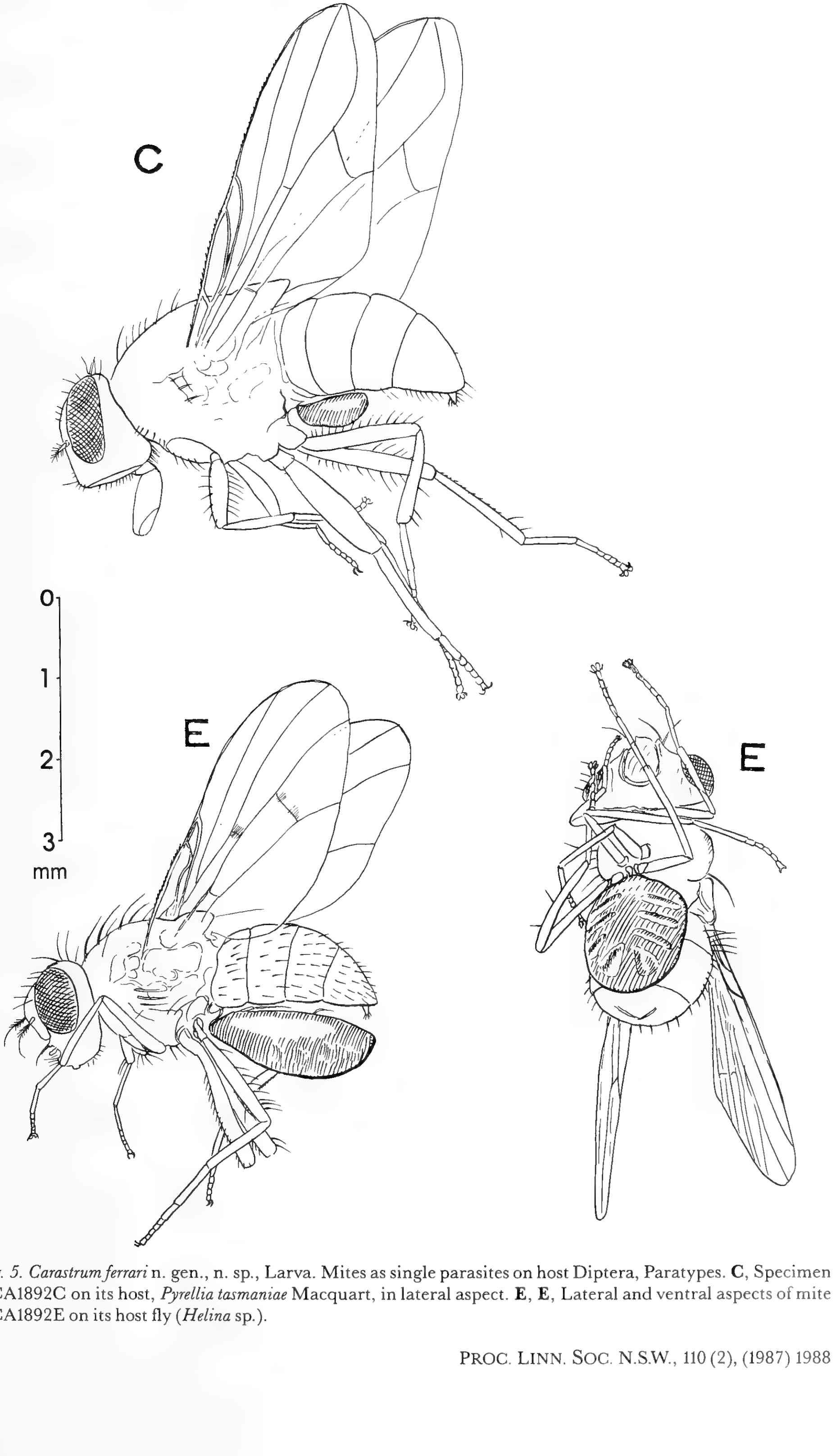

Fig. 5. Carastrum ferrari n. gen., n. sp., Larva. Mites as single parasites on host Diptera, Paratypes. **C**, Specimen ACA1892C on its host, *Pyrellia tasmaniae* Macquart, in lateral aspect. **E**, **E**, Lateral and ventral aspects of mite ACA1892E on its host fly (*Helina* sp.).

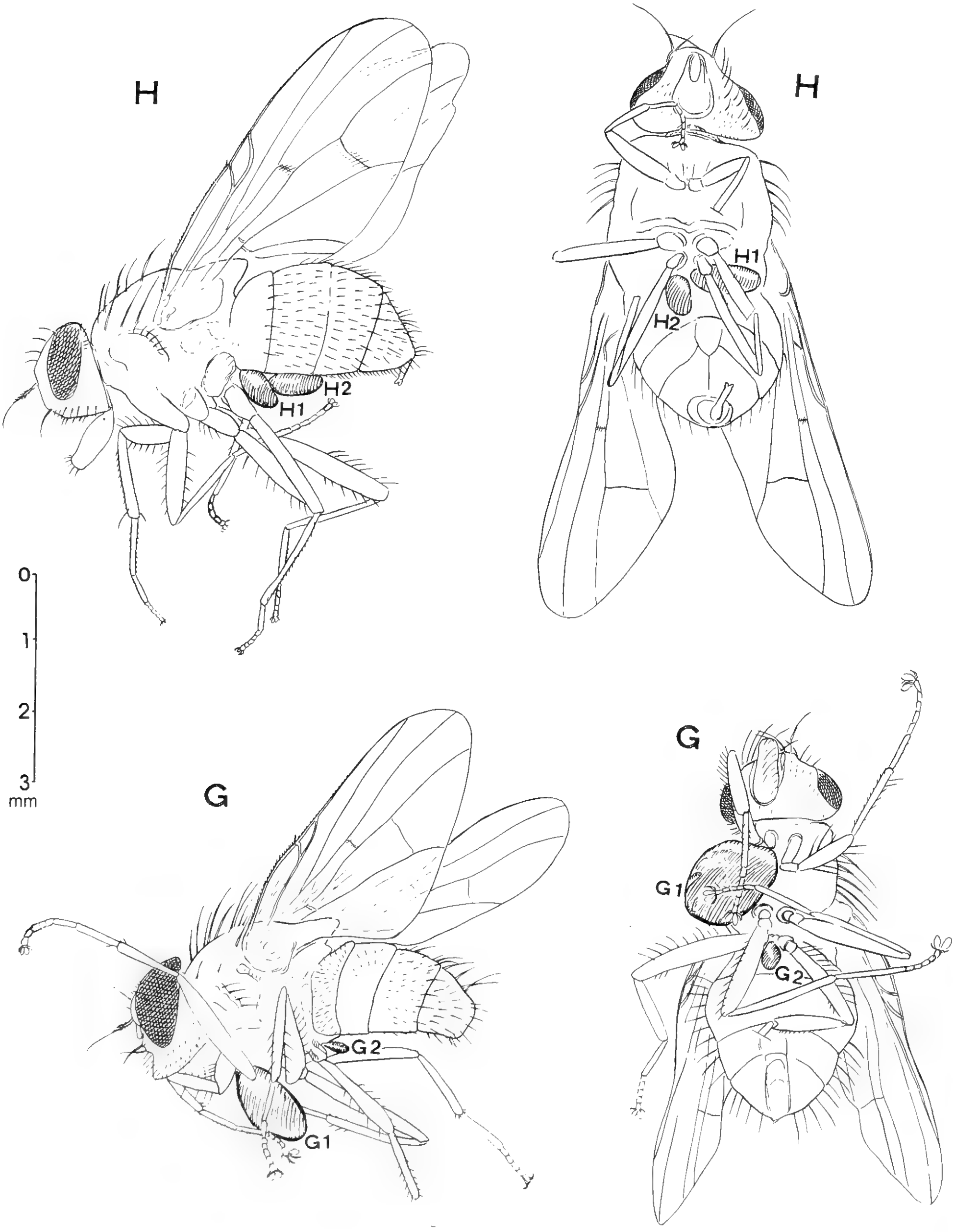

Fig. 6. Carastrum ferrari n. gen., n. sp., Larva. Host Diptera (*Helina* sp.) each with two mite ectoparasites. **H**, **H**, Lateral and ventral views of Paratypes ACA1892H1, H2 attached to metasternal-abdominal tergite I membrane. **G**, **G**, Lateral and ventral aspects of host fly with Holotype ACA1892G2 attached to metasternal-abdominal tergite I membrane, and with Paratype ACA1892G1 attached to prosternum.

Tribe CHARLETONIINI Southcott

This name was proposed in a key by Southcott (1961b, p. 522), but otherwise has not been formally defined. The following can now be submitted:

Definition

Adults: Callidosomatinae without distal tubercles on pedal tibiae.

Larvae: Callidosomatinae with scutalae 2+2 or 3+3. Pedocoxalae 1, 1, 1 or 2, 2, 2. Pedotrochanteralae 1, 1, 1 or 2, 2, 2. Posterior pedotibial claw hooklike or not. Palpal tibial claw (odontus) with or without accessory peg or basal process.

Type genus *Charletonia* Oudemans, 1910.

Comment: Adult Charletoniini can be separated from the Callidosomatini by a single criterion, i.e. by the absence of distal tubercles on pedal tibiae (see, however, some North American exceptions mentioned earlier). In the larvae so far allotted to the Charletoniini, only one genus has been experimentally correlated with its adult or deutonymphal instar, that being *Charletonia*, founded by Oudemans on 1 May 1910, and its post-larval instars being described under *Sphaerolophus* Berlese, founded on 1 July 1910. Correlations have been made by Ishii (in Southcott, 1961b, p. 528) and by Rosa and Flechtmann (1980) and Treat (1980). The other genera founded on larvae, *Hauptmannia* Oudemans, 1910, *Andrevella* Southcott, 1961, *Grandjeanella* Southcott, 1961 and *Pussardia* Southcott, 1961, may be tentatively allotted to the Charletoniini on present evidence. All of them come within the definition of Charletoniini as given above, and are excluded from the Callidosomatini as defined earlier in this paper. Further placements of these genera will probably need to depend on the evidence of experimental larva-postlarval instar correlations.

ACKNOWLEDGEMENTS

I am indebted to Mr Paul Ferrar, formerly of CSIRO Division of Entomology, Canberra, A.C.T., for the specimens, and to Dr D. H. Colless, CSIRO Division of Entomology, for the identifications of the host Diptera.

I thank the Australian Biological Resources Study for support.

References

BERLESE, A., 1888. — Acari Austri-Americani quos collegit Aloysius Balzan. *Boll. Soc. Ent. Ital.* 20: 171-222.

——, 1910. — Brevi diagnosi di generi e specie nuovi di Acari. *Redia* 6 (2): 346-388.

MULLEN, G. R., 1975. — Acarine parasites of mosquitoes. I. A critical review of all known records of mosquitoes parasitized by mites. *J. med. Entomol.* 12 (1): 27-36.

OUDEMANS, A. C., 1910. — Acarologische Aanteekeningen XXXII. *Ent. Ber., Amst.* 3 (53): 67-74.

RESH, V. H., and HAAG, K. H., 1974. — New records of parasitism of caddisflies by erythraeid mites. *J. Parasitol.* 60 (2): 382-383.

ROSA, A. E., and FLECHTMANN, C. H. W., 1980. — *Sphaerolophus* a synonym of *Charletonia*? (Acari: Erythraeidae). *Internat. J. Acarol.* 6 (3): 215-217.

SHARMA, G. D., DROOZ, A. T., and TREAT, A. E., 1983. — A new species of *Callidosoma* (Acari: Prostigma [sic]: Erythraeidae) parasite on adults of *Anacamptodes vellivolata* (Lepidoptera: Geometridae) as a larva, and predator of eggs of Lepidoptera as deutonymph and adult. *Ann. Entomol. Soc. America* 76 (1): 120-129.

——, FARRIER, M. H., and DROOZ, A. T., 1983. — Life-history, and sexual differences of *Callidosoma metzi* Sharma, Drooz and Treat (Acarina: Erythraeidae). *Internat. J. Acarol.* 9 (3): 149-155.

SOUTHCOTT, R. V., 1946. — Studies on Australian Erythraeidae (Acarina). *Proc. Linn. Soc. N.S.W.* 71 (1-2): 6-48.

——, 1957. — The genus *Myrmicotrombium* Womersley 1934 (Acarina, Erythraeidae), with remarks on the systematics of the Erythraeoidea and Trombidioidea. *Rec. S. Aust. Mus.* 13 (1): 91-98.

——, 1961a. — Notes on the genus *Caeculisoma* (Acarina: Erythraeidae) with comments on the biology of the Erythraeoidea. *Trans Roy. Soc. S. Aust.* 84: 173-178.

——, 1961b. — Studies on the systematics and biology of the Erythraeoidea (Acarina), with a critical revision of the genera and subfamilies. *Aust. J. Zool.* 9 (3): 367-610.

——, 1961c. — Description of two new Australian Smarididae (Acarina), with remarks on chaetotaxy and geographical distribution. *Trans Roy. Soc. S. Aust.* 85: 133-153.

——, 1966. — Revision of the genus *Charletonia* Oudemans (Acarina: Erythraeidae). *Aust. J. Zool.* 14 (4): 687-819.

——, 1972. — Revision of the larvae of the tribe Callidosomatini (Acarina: Erythraeidae) with observations on post-larval instars. *Aust. J. Zool., Suppl. Ser.* 13: 1-84.

——, 1986. — Studies on the taxonomy and biology of the subfamily Trombidiinae (Acarina: Trombidiidae) with a critical revision of the genera. *Aust. J. Zool., Suppl. Ser.* 123: 1-116.

TREAT, A. E., 1975. — *Mites of moths and butterflies*. Ithaca and London: Comstock Publishing Associates, Cornell University Press.

——, 1980. — Nymphal *Sphaerolophus* reared from larval *Charletonia* (Acarina: Erythraeidae). *Internat. J. Acarol.* 6 (3): 205-214.

——, 1985. — Larval *Callidosoma* (Acari, Erythraeidae): new records and a new rearing from the Americas. *Internat. J. Acarol.* 11 (2): 93-124.

WELBOURN, W. C., — 1983. — Potential use of trombidioid and erythraeoid mites as biological control agents of insect pests, pp. 103-140, *in* HOY, M. A., CUNNINGHAM, G. L., and KNUTSON, L., (eds), *Biological control of pests by mites*. Berkeley: Univ. Calif., Spec. Publicn. 3304.

WOMERSLEY, H., 1934. — A revision of the trombid and erythraeid mites of Australia with descriptions of new genera and species. *Rec. S. Aust. Mus.* 5 (2): 179-254.

——, 1936. — Additions to the trombidiid and erythraeid acarine fauna of Australia and New Zealand. *J. Linn. Soc. Lond. (Zool.)* 40 (269): 107-121.

The Lichen Genus *Cladonia* Section *Cocciferae* in Australia

A. W. ARCHER

ARCHER, A. W. The lichen genus *Cladonia* section *Cocciferae* in Australia. *Proc. Linn. Soc. N.S.W.* 110 (2), (1987) 1988: 205-213.

Eight species of *Cladonia* Hill ex Browne sect. *Cocciferae* (Delise) Dahl occur in Australia. *C. angustata* Nyl. is reported for the first time in Australia. A key to the species is presented and the major phenolic compounds of each taxon are reported.

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KEY WORDS: *Cladonia angustata* Nyl., *Cladonia bimberiensis* A. W. Archer, *Cladonia floerkeana* (Fr.) Flörke, *Cladonia macilenta* Hoffm., *Cladonia murrayi* W. Martin, *Cladonia pleurota* (Flörke) Schaerer, *Cladonia subdigitata* Nyl., *Cladonia weymouthii* F. Wilson ex A. W. Archer, lichens, *Cocciferae, Ochroleucae*, chemotaxonomy, distribution, Australian lichens.

INTRODUCTION

The lichen genus *Cladonia* Hill ex Browne contrains about 350 species (Ahti, 1982) and of these 53 are thought to occur in Australia. This paper describes the Australian species that form the section *Cocciferae* (Delise) Dahl, including the group *Ochroleucae* (Dahl, 1952). The study is based on an examination of relevant type specimens (indicated by !), specimens from Australian herbaria, Australian specimens in the British Museum (Natural History) (BM) and the University of Helsinki (H), and the author's own collections. No previous publication has dealt with this group of lichens in Australia but a recent paper (Stenroos, 1986) has described section *Cocciferae* from Melanesia, including Papua New Guinea. The following sixteen taxa of *Cladonia* sect. *Cocciferae* have previously been reported from Australia: *C. bacillaris* Nyl. (Watts, 1903), *C. bimberiensis* A. W. Archer (Archer, 1985), *C. coccifera* (L.) Willd. as *Cenomyce coccifera* (Brown, 1814), *C. corallifera* (Kunze) Nyl. (Krempelhuber, 1880), *C. cornucopioides* (L.) Hoffm. (Leighton, 1867), *C. deformis* (L.) Hoffm. as *Cenomyce deformis* (Brown, 1814), *C. didyma* (Fee) Vainio (Vainio, 1887: 139), *C. digitata* (Leighton, 1867), *C. flabelliformis* Vainio (Vainio, 1887: 116), *C. floerkeana* (Fr.) Flörke (Krempelhuber, 1880), *C. macilenta* Hoffm. (Krempelhuber, 1880), *C. murrayi* W. Martin as *Cenomyce firma* (Laurer, 1827), *C. muscigena* Eschw. (Krempelhuber, 1880), *C. pleurota* (Flörke) Schaerer as *C. coccifera* var. *pleurota* (Vainio, 1887: 170), *C. subdigitata* Nyl. (Vainio, 1887: 181) and *C. weymouthii* F. Wilson ex A. W. Archer (Archer, 1985). Several of these reports are not valid and are probably based on misidentifications of other species; eight species in Section *Cocciferae* are here reported to occur in Australia. A description of each species is given together with its chemistry and distribution.

SYSTEMATICS AND DISCUSSION

Cladonia sect. *Cocciferae* (Delise) Dahl

Rev. Bryol. Lichenol. 21: 121 (1952) *Cenomyce* [rankless] *Cocciferae* Delise in Duby, *Bot. gall.* 2: 632 (1830).

Podetia scyphose or escyphose, simple or slightly branched, often sorediate. Apothecia red, containing rhodocladonic acid, or pale brown. The major phenolic compounds are usnic, iso-usnic, thamnolic, barbatic, didymic, and squamatic acids; the yellow pigment skyrin and the triterpene zeorin may also be present.

KEY to the species of *Cladonia* sect. *Cocciferae* in Australia

1.	Podetia escyphose	2
1.	Podetia scyphose	6
2.	Usnic acid present	3
2.	Usnic acid absent	4
3.	Podetia with variable soredia; didymic acid present	*C. angustata*
3.	Podetia with dense farinose soredia; didymic acid absent	*C. bimberiensis*
4.	Podetia corticate, or partly corticate and granular sorediate	*C. floerkeana*
4.	Podetia partly corticate and farinose sorediate	5
5.	Podetia corticate only at base and just below apothecia; apothecia common; usually less than 25mm tall	*C. macilenta*
5.	Podetia partly corticate, the cortex often covering the lower third of the podetia; apothecia rare; usually more than 30mm tall	*C. weymouthii*
6.	Podetia Pd-, thamnolic acid absent; apothecia rare	*C. pleurota*
6.	Podetia Pd+ yellow, thamnolic acid present; apothecia common	7
7.	Usnic acid absent; basal squamules conspicuous, podetia green, growing on soil	*C. murrayi*
7.	Usnic acid present; basal squamules inconspicuous, podetia yellow, growing on wood	*C. subdigitata*

Cladonia angustata Nyl., *Ann. Sci. Nat. Bot.* sér. 4, 11: 236 (1859). *Cladonia cornucopioides* var. *angustata* Nyl., *Mém. Soc. Sci. Nat. Cherbourg* 5: 96 (1858 ('1857')), nom. nud.
Type: Iles Sandwich (Hawaii), J. Remy 1851-1855; lectotype: H-NYL 37978!; isolectotype: PC.

Description: Basal squamules evanescent or persistent, 1 × 1.5mm, lacinate or crenate, esorediate, yellowish-green above, white below. Podetia growing from the basal squamules, 5-10mm tall, 0.5-1.0mm diam., escyphose, simple or rarely branching, apices obtuse or sub-acute, the basal area corticate, the remainder ecorticate and sorediate, soredia farinose to granular, cortex sub-continuous or areolate. Apothecia red, terminal.

Chemistry: K+ yellow or K-, KC+ yellow, P+ yellow or P-. Usnic and didymic acids ± thamnolic ± barbatic acids.

The well-defined basal corticate area on the podetia and the presence of usnic and didymic acids together, distinguish this species from other Australian taxa in the group Cocciferae. Mature apothecia were not seen in Australian specimens.

Distribution: Cladonia angustata is an uncommon but widely distributed species in Western Australia, Queensland and Tasmania where it grows on dead wood or sandy peat. It also occurs in New Zealand, Japan and Hawaii.

Representative specimens: Western Australia: Busselton, Layman Rd, near Wonnerup House, 31.xii.1981, N. Sammy (PERTH 820560); Porongerups National Park, near summit of Nancy Peak, 7.vii.1968, N. Sammy (PERTH 840899); Jarrahdale, 50km SE of Perth, 9.vi.1973, N. Sammy (PERTH 840934). Queensland: Wybara, 9km NW of Wallanagara, H. Streimann 9829 (CBG). Tasmania: Mawbanna Plain, 15km SE of Stanley, G. Kantvilas 1.iv.1985 (H).

Cladonia bimberiensis A. W. Archer, *Muelleria* 6: 93 (1985).
Type: Mt Bimberi, 49km SW of Canberra, A.C.T., H. Streimann 9743; holotype: CBG!; isotype: H!, US.
Description: Basal squamules persistent, 0.5-1.0mm long, 0.3-0.5mm wide, esorediate, yellow-green above, white below, margins crenate. Podetia growing from the basal squamules, 10-30mm tall, 0.7-2.0mm diam., pale yellow, more or less cylindrical, simple and escyphose, or with shallow, deformed scyphi with marginal proliferations; podetia rough corticate at the base and then becoming ecorticate and densely farinose sorediate, with the interior of the scyphi farinose sorediate; esquamulose or occasionally with squamules on the lower part of the podetia. Apothecia not seen; pycnidia subconical, brown, 0.1-0.2mm diam., 0.3-0.4mm long, terminal or marginal on the scyphi; conidia not seen.
Chemistry: K-, KC+ yellow, P-. Usnic, barbatic and 4-0-demethyl barbatic acids.

C. bimberiensis is distinguished from *C. macilenta* and *C. corniculata*, by the yellow colour and the K- and P- reactions, and from *C. angustata* by the branched podetia and the absence of didymic acid.
Distribution: Cladonia bimberiensis is an uncommon alpine to subalpine species found in Victoria, the Australian Capital Territory and Tasmania where it grows on dead wood. It also occurs in the South Island of New Zealand.
Representative specimens: Australian Capital Territory: SE of Bimberi Park, Bimberi Range, J. A. Elix 6640 (ANUC, MEL 1047742); ibid. J. A. Elix 6639 (NSW); Mt Franklin, A. Archer 1900 (ANUC, H, NSW). Victoria: track to Mt Stirling summit, A. Archer 2058 (NSW). Tasmania: North East Great Lake, G. Bratt 564 (BM).

Cladonia floerkeana (Fr.) Flörke, *Clad. Comment.* 99 (1828). (*'Floerkiana'*).
Cenomyce floerkeana Fr., *Lich. Suec. Exsic.* 82 (1824).
Type: not designated.
Description: Basal squamules small, inconspicuous, 0.5-1 × 1-2mm slightly lobed. Podetia growing from the basal squamules, simple or sparingly branched near the apices, escyphose, sterile podetia subulate, 5-20(rarely to 25)mm tall, 0.5-1(rarely to 2)mm diam., the major part of the podetia and the area below apothecia corticate, the cortex scabrose to sub-verrucose, the remainder ecorticate and minutely squamulose or granular sorediate, or the podetia completely corticate. Apothecia common, red, convex, terminal, 1-2mm diam.
Chemistry: K+ yellow or K-, KC-, P+ yellow or P-. Barbatic and didymic acids ± thamnolic acid.

Cladonia floerkeana is a widely distributed and, when fertile, conspicuous species in Eastern Australia, distinguished from *Cladonia macilenta* by the predominantly corticate podetia and the absence of farinose soredia. In contrast to specimens from the Northern Hemisphere the Australian specimens often contain thamnolic acid.
Distribution: Cladonia floerkeana is a cosmopolitan species growing on dead or burnt wood or on soil. It occurs in eastern Queensland, New South Wales, Australian Capital Territory, Victoria, South Australia and Tasmania, and also on Norfolk Island.
Representative specimens: South Australia: Mt Lofty Range, 5.x.1971, D. Whibley 3678 (AD 97647213). Queensland: 1km S of Herberton, J. Elix 16614 (ANUC). New South Wales: 25km E of Braidwood, 15.xi.1970, E. Dahl (CANB 227864); near Yeomans Bay, ca 30km N of Sydney, 30.iii.1985, A. Archer 1741 (H, NSW). Australian Capital Territory: Jervis Bay, H. Streimann 3574 (CBG, H). Victoria: near Beaconsfield, G. Bratt 69/611 (HO 53117). Tasmania: Churchill Spur, Florentine River, G. Bratt 68/237 (HO 53877). Norfolk Island: J. & T. Gilbert, s.n. (HO 53167).

Cladonia macilenta Hoffm. *Deutschl. Fl.* 2: 126 (1796).
Type: not designated.
Cladonia bacillaris Nyl., *Not. Sallsk. Fauna Fl. Fenn. Förh.* 8: 179 (1866).
Type: not designated.
Description: Basal squamules small, inconspicuous, 0.5 × 1mm, margins ± soredia. Podetia growing from the basal squamules, simple or rarely branching near the apices, escyphose, pale green, 10-20(rarely to 30)mm tall, 0.5-1.5mm diam., the major part of the podetia ecorticate and farinose sorediate apart from short, smooth corticate areas at the base and below the apothecia; sterile podetia blunt or subulate; rarely squamulose on the basal corticate area. Apothecia red, convex, terminal, 0.5-2mm diam.
Chemistry: K+ yellow or K-, KC-, P+ yellow or P-. Barbatic, ± didymic ± thamnolic acids or rarely squamatic and consquamatic acids.

Cladonia macilenta is distinguished from *Cladonia weymouthii* by the short, rarely branched podetia and the small corticate area at the base of the podetia. It is distinguished from *Cladonia floerkeana* by the conspicuously ecorticate and farinose sorediate podetia. The exact status of *Cladonia bacillaris* as a separate species is unclear (Ahti, 1980). Christensen (1987) has recently suggested that *Cladonia bacillaris* is merely a thamnolic acid deficient form of *Cladonia macilenta.* However, in Australia specimens lacking thamnolic acid are uncommon and squamatic acid has only been found in one specimen from Victoria.
Distribution: Cladonia macilenta is a cosmopolitan species growing on dead wood or on soil. It occurs in south western Western Australia, eastern Queensland, New South Wales, Australian Capital Territory, and Victoria.
Representative specimens: With thamnolic acid: Western Australia: Porongorups National Park, 15.x.1980, N. Sammy (PERTH 810103). Queensland: Tinnaroo Falls Rd, 12km NE of Atherton, J. Elix 16584 (ANUC). New South Wales: Clyde Mtn, 8.xii.1974, J. Elix (ANUC, MEL 1017163); Bolivia Hill, near Deepwater, 23.i.1980, H. Streimann 9953 (CBG 8002514, H). Victoria: near Moondarra, G. Bratt 76/509 (HO 52909).

Lacking thamnolic acid: New South Wales: South Tinderry Peak, 22.iii.1970, E. Dahl (CANB 227672); Mt Banks, 9.iii.1985, A. Archer 1736 (NSW); near Frederica Falls, Lawson, 27.vi.1987, A. Archer 2115 (NSW). Australian Capital Territory: near Honeysuckle Creek Tracking Station, 2.iv.1983, A. Archer 1483 (NSW).

With squamatic acid: Victoria: by the side of Buller Creek, Mirimbula, 5.xi.1986, A. Archer 2049 (H, NSW).

Cladonia murrayi W. Martin, *Trans Roy. Soc. N.Z., Bot.* 2: 40 (1962).
Type: Secretary Island, Doubtful Sound, West Otago, New Zealand, Feb. 1959, J. Murray; holotype: CHR 257075!; isotype: BM!.
Cenomyce firma Laurer, *Linnaea* 2: 44 (1827); *Cladonia firma* (Laurer) Krempelh., *Verh. zool.-bot. Ges. Wien*, 18: 309 (1868), nom. illeg.;
Cladonia firma (Laurer) Vainio, *Acta Soc. Fauna Flora fenn.* 4: 215 (1887), nom. inval., non *Cladonia firma* (Nyl.) Nyl., *Bot. Ztg.* 47: 352 (1861).
Type: New Holland, F. Sieber, sin. loc. [?Tasmania]; holotype: G!.
Description: Basal squamules persistent, conspicuous, 1-2mm wide, 3-6mm long, incised, esorediate, the lower surface becoming yellow to yellow-brown in the older parts. Podetia growing from the squamules, 1-2.5cm tall, 1-3mm diam., green or greyish-green, scyphose or with deformed scyphi, with short (2-4mm) proliferations bearing apothecia, corticate, verrucose to scaly, becoming ecorticate and squamulose, esorediate. Apothecia conspicuous, red, 1-3(rarely to5)mm diam.
Chemistry: K+ yellow, KC-, P+ yellow. Thamnolic acid and skyrin (rhodophyscin).

Cladonia murrayi is a terricolous, corticate, green, scyphose species with conspicuous red apothecia. It is distinguished from *Cladonia subdigitata* by the green scyphi and the absence of usnic acid. The exact origin of the type specimen of *Cenomyce firma* is unclear. The Austrian collector Franz Sieber collected in New South Wales (Audas, 1950: 21) but did not visit Tasmania (Kantvilas, 1983). Recent collections of *Cladonia murrayi* have been made only in Tasmania and New Zealand and no specimens are known from New South Wales. Herbarium specimens labelled *Cladonia murrayi* from Mt Wilhelm, New Guinea (R. Hnatiuk and E. Dahl, 26.viii.1970) lacked thamnolic acid and skyrin and are identified as *Cladonia pseudodigitata* Gyeln. (CANB 227807) and *Cladonia yunnana* (Vainio) des Abb. (CANB 227808).

Distribution: *Cladonia murrayi* occurs in Tasmania, growing on moist soil in semi-shaded positions, with *Cladia aggregata* (Sw.) Nyl. and *Siphula decumbens* Nyl. It also occurs in New Zealand.

Representative specimens: Tasmania: Ben Lomond, May 1887, Dr Bamford (NSW); near summit of Mt Murchison, Dec 1893, Fitzgerald (NSW); Lake Dobson, Mt Field National Park, G. Kantvilas 613/81 (BM); Great Dome, Dennison Range, G. Kantvilas 778/81 (BM); W side of Lake Dove, 30.xi.1983, A. Archer 1562A (H, NSW); 8km from Lake Dobson, G. Bratt 70/303 (HO 56284).

Cladonia pleurota (Flörke) Schaerer, *Enum. lich. eur.*: 186 (1850).

Capitularia pleurota Flörke, *Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk.* 2: 218 (1808); *Cladonia coccifera* var. *pleurota* (Flörke) Schaerer, *Lich. helv. spic.*: 25 (1823).

Type: not designated.

Cladonia cornucopioides var. *grandis* Krempelh., *Verh. zool.-bot. Ges. Wien* 30: 332 (1881).

Type: Mt Ellery, Gippsland, Victoria, 1870, C. Walter; holo: M!.

Description: Basal squamules persistent or evanescent, inconspicuous, 1-2mm wide, 2-4mm long, irregularly crenate to lobate. Podetia growing from the basal squamules, simple, scyphose, scyphi 1-4cm tall, 4-10mm diam, with marginal proliferations with apothecia, or in the form of scyphi; the interior of the scyphi ecorticate with granular soredia or tiny flattened corticate scales; the base of the podetia corticate, the cortex continuous or areolate, becoming verrucose and scaly to subsquamulose, finally ecorticate and granular sorediate in the upper parts. Apothecia red, convex, 1-3mm diam, solitary or clustered on the margins of the scyphi, or pedicellate on the margins of the scyphi, rarely seen in Australian specimens.

Chemistry: K-, KC+ yellow, P-. Usnic and iso-usnic acids and zeorin.

Cladonia pleurota is a common scyphose species and was one of the first *Cladonia* species collected in Australia by Robert Brown (Crombie, 1880). The presence of iso-usnic acid and the partly corticate scyphi distinguish *C. pleurota* from all other Australian species of *Cladonia* whilst the absence of minutely farinose soredia differentiates it from *C. deformis*. Specimens from Tasmania are often 2-4cm tall.

Distribution: *Cladonia pleurota* is a widely distributed species found on soil in all Australian states except South Australia. It also occurs on Macquarie Island and in New Zealand, Europe, North America and Japan.

Representative specimens: Western Australia: Porongorups National Park, 18.x.1980, N. Sammy (PERTH 810019). New South Wales: South Tinderry Peak, 22.iii.1970, E. Dahl (CANB 227853); 2km NE of Mt Kosciusko, 14.iii.1979, H. Streimann 7631 (CBG 7907333, H, US). Australian Capital Territory: Black Mountain, 30.vii.1975, B. Hain 40 (CBG 8004587). Victoria: Mt Buffalo, 14.xi.1979, A. Archer 830 (H). Tasmania: Mons Tabulans [Mt Wellington] R. Brown 530 (BM); Arthurs Pass, G. Bratt 72/1810

(HO 53142). Macquarie Island: 1 mile N of Bauer Bay, 28.i.1964, R. Filson 5812 (MEL 20278).

Cladonia subdigitata Nyl., *C. r. hebd. Séanc. Acad. Sci.*, Paris 83: 88 (1876).
Type: Campbell Is, New Zealand, 1874, Filhol; lectotype: H-NYL 37858! (T. Ahti, in litt.); isolectotype: MEL!; syntypes: BM!, PC, TUR-V 14155, 14157, n.v.
Cladonia corallifera (Kunze) Nyl. subsp. *subdigitata* Vainio, *Acta Soc. Fauna Flora fenn.* 4: 180 (1887).
Type: not designated.
Cladonia deformis (L.) Hoffm. var. *tasmanica* Krempelh., *Verh. zool.-bot. Ges. Wien* 30: 332 (1881).
Type: Tasmania, J. v. B. Gulliver [T. & B. Gulliver]; holotype: M!; isotype: MEL!.
Description: Basal squamules pale yellow, persistent, inconspicuous, 1-3 × 1-3mm, subpalmate, margins crenate, esorediate. Podetia growing from the basal squamules, yellow, simple, scyphose, widening gradually from the base, 1.5-3.0(rarely to 5.0)cm tall, 1.5-4mm diam., corticate at the base, becoming scaly or rough or minutely squamulose, corticate below apothecia, scyphi 3-5(rarely to 8)mm diam., interior corticate, closed, or open in older specimens, with marginal scyphi or apothecia. Apothecia red, conspicuous, common, convex, 1-4mm diam., marginal on the scyphi or on corticate proliferations from the margins of the scyphi.
Chemistry: K+ yellow, KC+ yellow, P+ yellow. Usnic and thamnolic acids ± skyrin.

Cladonia subdigitata is distinguished from all other Australian scyphose *Cladonia* by the yellow scyphi with conspicuous red apothecia and the presence of thamnolic acid. This taxon is often misidentified as *Cladonia coccifera* (L.) Willd. on herbaria labels.
Distribution: Cladonia subdigitata is a conspicuous, scyphose species growing on dead wood. It occurs in Tasmania and rarely in Victoria, and has been reported from the Grampians, Victoria (Vainio, 1887) and from Papua New Guinea (Mattick, 1942) but this last report was not confirmed (Stenroos, 1986). It also occurs on Macquarie Island and in New Zealand.
Representative specimens: Victoria: Lake Tyers, Feb. 1888, F. Wilson (NSW); Mt Macedon, R. Filson 12041 (MEL 39956). Tasmania: Mt Dromedary, June 1895, L. Rodway (NSW); Federation Peak, Jan. 1949, J. Béchervaise (MEL 7106); Mt Mueller, G. Bratt 73/121 (HO 44688); Mt Hartz, G. Bratt 3083 (HO 44721); Lake Fenton, G. Bratt 461 (HO 56247). Macquarie Island: 1 mile N of Bauer Bay, 28.i.1964, R. Filson 5832 (MEL 20277).

Cladonia weymouthii F. Wilson ex A. W. Archer, *Muelleria* 6: 94 (1985).
Type: Huon River, Tasmania, 5 Feb. 1892, W. A. Weymouth; holotype: MEL 6760!; isotype: NSW!.
Cladonia cornucopioides L. f. *arrosa* F. Wilson, *Pap. Proc. Roy. Soc. Tasm.* 1892-3: 151 (1893).
Type: Brown's Track, Mt Wellington, Tasmania, F. Wilson, no date; holotype: NSW L4388!.
Description: Basal squamules inconspicuous, persistent, 0.5-1mm wide, 1-2mm long, incised, esorediate, margins crenate. Podetia arising from the basal squamules, 1.5-5.0cm tall, 1-4mm diam., green to greenish-grey, subcylindrical or tapering to the apices, simple or branching somewhat near the tips, the branching forming deformed scyphi, lacking well-defined scyphi, axils closed; podetia corticate at the base and for one third of the length of the podetia, and below the apothecia, the remainder of the podetia ecorticate and densely farinose sorediate; podetia esquamulose or with squamules on the lower part. Apothecia rare, terminal, red, convex, 1-3mm diam.

Chemistry: K- or K+ yellow, KC-, P- or P+ yellow. Thamnolic, barbatic and didymic acids; thamnolic and/or didymic acids may be absent.

Cladonia weymouthii resembles *Cladonia macilenta* but is distinguished from that species by the occasional deformed scyphi and the tall, branched, partly corticate podetia. It is distingushed from *Cladonia corniculata* by the absence of fumarprotocetraric acid.

Distribution: Cladonia weymouthii is an uncommon species growing on dead or decayed wood. In Australia it is known only from Tasmania, at altitudes from 250m to 1800m. It also occurs in New Zealand, Papua New Guinea and the Solomon Islands.

Representative specimens: Tasmania: Price's Rivulet, Huon, Feb. 1902, W. A. Weymouth (NSW); near Hastings Cave, 27.xi.1982, A. Archer 1417D (H, MEL 1045447); 15km W of Maydena, 7.xii.1983, A. Archer 1545A (CBG, NSW); Pencil Pine Creek, 29.xi.1983, A. Archer 1566A (MEL 1045448); the Hermit, 8km SE of Strathgordon, 19.i.1984, G. Kantvilas 59/84 (NSW); Mt Wellington, J. Townrow 34 (HO 54026).

EXCLUDED AND DOUBTFUL SPECIES

Cladonia bacillaris Nyl.

The status of *C. bacillaris* as a separate species has been discussed by Ahti (1980), Ahti and Stenroos (1986) and Christensen (1987); following Christensen, *C. bacillaris* is here included in *C. macilenta.*

Cladonia coccifera (L.) Willd. em. Asah. *Fl. berol. Prod.*: 361 (1787).
Lichen cocciferus L., *Sp. pl.:* 1151 (1753).

C. coccifera usually contains usnic and barbatic acids. Although reported to occur in Autralia (Krempelhuber, 1880; Vainio, 1887: 154) no specimens corresponding to *C. coccifera* have been found. Australian specimens in herbaria labelled *'C. coccifera'* are often fertile *C. subdigitata* but specimens of *C. murrayi, C. pleurota* and *C. merochlorophaea* Asah. have also been identified as *C. coccifera.*

Cladonia corallifera (Kunze) Nyl. *Flora,* Jena 57: 70 (1874).
Cenomyce corallifera Kunze, printed herbarium label with description (?1827).

C. corallifera, a scyphose species containing usnic, thamnolic and didymic acids, is primarily a lowland Amazonian species from South America (Ahti and Stenroos, 1986). The reported occurrence in Australia is probably based on a misidentification of *C. subdigitata*, which lacks didymic acid.

Cladonia cornucopioides (L.) Hoffm. *Deutsch. Fl.* 2: 128 (1796).
Lichen cornucopioides L., *Sp. pl.* 1151 (1753).

C. cornucopioides is a later synonym of *C. coccifera* (Vainio, 1887: 149). *C. cornucopioides* var. *grandis* Krempelh. (Krempelhuber, 1881) from Victoria was found to be *C. pleurota* (Acher, 1986b). *C. cornucopioides* f. *arrosa* (Wilson, 1893) from Mt Wellington, Tasmania, NSW L4388, contained only thamnolic acid and is *Cladonia weymouthii*, vide supra.

Cladonia deformis (L) Hoffm. *Deutsch. Fl.* 2: 120 (1796).
Lichen deformis L., *Sp. pl.: 1152 (1753).*

Cladonia deformis is morphologically similar to *C. pleurota* and both taxa contain usnic and iso-usnic acids and zeorin. Australian specimens identified as *C. deformis*, including the early collection by R. Brown from Tasmania, lack the minutely farinose soredia characteristic of this taxon and these specimens are now referred to *C. pleurota.* No Australian material resembling northern hemisphere specimens of *C. deformis* has been found among the specimens examined. *C. deformis* var. *tasmanica* Krempelh. was referred to *C. subdigitata* (Archer, 1986b).

Cladonia didyma (Fée) Vainio. *Acta Soc. Fauna Flora fenn.* 4: 137 (1887).
Scyphophorus didymus Fée, *Essai Crypt.*: CI (1825).

C. didyma, containing thamnolic, barbatic and didymic acids, is a widely distributed pan-tropical to pan-temperate species; the total distribution was recently reported to include Australia (Stenroos, 1986). This record was based on the inclusion of *C. didyma* in a tentative Key to Australian *Cladonia* (Archer, 1986a). A re-examination of Australian specimens determined as *C. didyma* has shown that they lack the ecorticate squamulose podetia characteristic of *C. didyma* so they are now included in *C. floerkeana.*

Cladonia digitata (L.) Hoffm. *Deutsch. Fl.* 2: 124 (1796).
Lichen digitatus L., *Sp. pl.*: 1152 (1753).

C. digitata is a scyphose species, with conspicuous basal squamules and containing thamnolic acid, found in Europe, North America and Japan. No material corresponding to *C. digitata* has been found amongst the collections examined in Australian herbaria. The records of *C. digitata* from Australia are probably based on misidentifications of *C. subdigitata*, which contains usnic acid. The detailed description of '*C. digitata*' provided by Wilson (1893) based on material from Mt Wellington, Tasmania could equally refer to *C. subdigitata.* A specimen with conspicuous basal squamules and labelled *C. digitata* from Sandringham, Victoria (NSW) contained atranorin and fumarprotocetraric acid and has been identified as *C. praetermissa* A. W. Archer. A second scyphose specimen, labelled '*Cladonia digitata*' from Waterfall, Tasmania (NSW) contains usnic and thamnolic acids and is identified as *Cladonia subdigitata.*

Cladonia flabelliformis Vainio. *Acta Soc. Fauna Flora fenn.* 4: 113 (1887).

C. flabelliformis is a later name for *C. polydactyla* (Flörke) Sprengel (Ahti, 1978). It is a sorediate, scyphose species containing thamnolic acid, which is widespread in western Europe (Tonsberg and Ahti, 1980). The Australian record is probably based on a misidentification of *C. subdigitata* as no specimens from Australia have been found corresponding to *C. polydactyla.*

Cladonia muscigena Eschw. *In* Martius, *Fl. Bras.* 1 (1): 262 (1833).

The type material of *C. muscigena* was collected in Brazil but the exact status of the species is uncertain (Stenroos, 1986). Vainio (1887) considered *C. muscigena* to be a variety of *C. didyma* and it is possible that the first and only report of *C. muscigena* from Australia was based on a misidentification of *C. floerkeana.* It is possible that the reports of *C. muscigena* occurring in New Caledonia are also based on misidentifications of *C. floerkeana* (Stenroos, 1986).

ACKNOWLEDGEMENTS

The author is grateful to Professor T. Ahti, Helsinki, for helpful discussion and to the National Herbarium of New South Wales for arranging the loan of specimens. Acknowledgement is made to the Director, Division of Analytical Laboratories, for permission to publish this paper.

References

AHTI, T., 1978. — Nomenclatural and taxonomic remarks on European species of *Cladonia*. *Ann. bot. fenn.* 15: 7-14.

——, 1980. — Nomenclatural notes on *Cladonia* species. *Lichenologist* 12: 125-133.

——, 1982. — Evolutionary trends in Cladoniiform Lichens. *J. Hattori Bot. Lab.* 52: 331-341.

——, and STENROOS, S., 1986. — A revision of Cladonia sect. Cocciferrae in the Venuzuelan Andes. *Ann. bot. fenn.* 23: 229-238.

ARCHER, A. W., 1985. — Two new lichens: *Cladonia bimberiensis* and *Cladonia weymouthii. Muelleria* 6: 93-95.

——, 1986a. — A tentative key to the lichen genus *Cladonia* in Australia. 10 pp. Sydney (mimeographed).

——, 1986b. — Nomenclatural notes on some Australian *Cladonia* species. *Lichenologist* 18: 241-246.

AUDAS, J. W., 1950. — *The Australian Bushland.* Melbourne: Robertson and Mullens Ltd.

BROWN, R., 1814. — A list of plants natives both of Terra Australia and of Europe. Appendix III, in FLINDERS, M., *A voyage to Terra Australis:* 592-594. London: G. and W. Nicol.

CHRISTENSEN, S., 1987. — Morphological and chemical variation in the *Cladonia macilenta/bacillaris* aggregate in Denmark. *Lichenologist* 19: 61-69.

CROMBIE, J. M., 1880. — Enumeration of Australian lichens in Herb. Robert Brown (Brit. Mus.), with descriptions of new species. *J. Linn. Soc. Lond. (Bot.)* 17: 390-401.

DAHL, E., 1952. — On the use of chemistry in lichen systematics. *Rev. bryol. lichenol.* 21: 119-134.

KANTVILAS, G., 1983. — A brief history of lichenology in Tasmania. *Pap. Proc. Roy. Soc. Tasm.* 117: 41-51.

KREMPELHUBER, A., 1880., — Lichenes australini e Baronis de Mueller collectionibus. *In* MUELLER, F., *Fragmenta phytographiae Australiae. Supplementum ad volumen undecimen.*: 70-74. Melbourne: Government Printer.

——, 1881. — Ein neuer Beitrag zur Flechtenflora Australiens. *Verh. zool.-bot. Ges. Wien* 30: 329-342.

LAURER, F., 1827. — Sieber'sche Lichenen. *Linnaea* 2: 38-46.

LEIGHTON, W. A., 1867. — Notulae Lichenologicae No. XII. On the *Cladoniei* in the Hookerian Herbarium at Kew. *Ann. Mag. nat. Hist.* 19: 99-124.

MATTICK, F., 1942. — Die Flechten von Neu-Guinea. 1. Allgemeines. Die Gattung *Cladonia.* In DIELS, L., Beiträge zur Flora von Papuasien XXVI. *Bot. Jb.* 72: 151-158.

MÜLLER ARGOVIENSIS, J., 1887. — Revisio Lichenum australiensium Krempelhuberi. *Flora,* Jena 70: 113-118.

STENROOS, S., 1986. — The family *Cladoniaceae* in Melanesia. 2. *Cladonia* section *Cocciferae. Ann. bot. fenn.* 23: 239-250.

TONSBERG, T., and AHTI, T., 1980. — *Cladonia umbricola*, a new lichen species from north west Europe and western North America. *Norw. J. Bot.* 27: 307-309.

VAINIO, E. A., 1887. — Monographia Cladoniarum Universalis. I. *Acta Soc. Faun. Fl. Fenn.* 4: 1-509.

WATTS, W. W., 1903. — Notes and Exhibits; twenty-seven lichens from determinations by Dr Bouly de Lesdain of Dunkerque. *Proc. Linn. Soc. N.S.W.* 28: 498-499.

WILSON, F. R. M., 1893. — Tasmanian Lichens Part 1. *Pap. Proc. Roy. Soc. Tasm. 1892:* 133-178.

Notes and Discussion

A dietary study of *Sillago analis* and its variation in three Australian locations

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The golden-lined whiting, *Sillago analis* (Whitley) is a macrobenthic carnivore widespread around the coast of Australia north of 30°S (McKay, 1985). Two previous studies of the diet of *S. analis* gave differing results. Lennanton (1969) reported that *S. analis*, feeding sub-littorally in a mangrove environment in Shark Bay (Western Australia), showed a strong preference for polychaete worms. Gunn and Milward (1985) found that *S. analis* caught from the beaches and estuaries around Townsville, fed predominantly on the bivalve mollusc *Mesodesma eltane*. The present study of *S. analis* collected from Deception Bay, SE Queensland (27°10′S. 153°00′E) reveals a further variation in the diet of this species.

120 *S. analis* were collected on six occasions between December and February (summer) of 1983/4, and 200 fish were collected on two occasions in June and July (winter) of 1984. The feeding habitat consisted of an intertidal seagrass flat with a zone of mangroves above mean tide level. Preliminary gut content analyses indicated that *S. analis* was a consistent nocturnal feeder in this habitat, and therefore collections were carried out at night. Fish were put on ice immediately on capture and had their stomachs excised and preserved in 10% formalin within one hour. Fish ranged in size from 119mm to 322mm (F.L.).

Stomach contents were examined using a stereo dissecting microscope where necessary. Most prey animals were identified to genus and many to species. Both numerical and weighted points methods were used to quantify the contribution of prey organisms to the diet of *S. analis*. The numerical method as described by Hynes (1950) gives an indication of the numbers of each prey type taken by the sampled population. In the case of the weighted points method, the procedure followed was a modification of that described by Hynes (1950). The volume of each food type was estimated by eye and expressed as a percentage of the total stomach contents volume. Items making up less than 5% of the total contents were recorded but were not allocated a points score. The points for each food type were then multiplied by a stomach fullness index assigned using the criteria of Ball (1961) to give weighted points values.

Table 1 lists the contribution of prey items to the diet of *S. analis* at Deception Bay from summer and winter samples. A wide variety of crustaceans was taken; however three crab species (*Macropthalmus setosus*, *M. punctulatus* and *Ilyograpsis paludicola*) predominated. A Wilcoxon test (Siegel, 1956) indicated that there was no significant difference between summer and winter diets. However, *Glauconome virens* siphon tips, which formed a major part of *S. analis'* winter diet, were not seen in summer samples. Plant material was only seen in small amounts and was probably ingested incidentally with prey items.

Gunn and Milward (1985) described the pharangeal dentition of *S. analis*. They concluded that the broad molariform pharangeal teeth in this species aided in the mastication and transport to the oesophagus of both hard and soft bodied prey types. In

TABLE 1

The percentage contribution of prey to the diet of Sillago analis *at Deception Bay*

Prey Category		Numerical Method		Weighted Points Method	
		Summer n = 120	Winter n = 200	Summer n = 120	Winter n = 800
CRUSTACEA		85.2	48.6	87.3	67.0
(a) Natant Decapoda					
Ocypodidae	*Macropthalmus setosus*	14.6	7.1	21.5	13.4
	M. punctulatus	21.4	11.6	19.2	14.5
	Uca sp.	0.3	0.5	1.2	1.3
Grapsidae	*Ilyograpsis paludicola*	32.5	12.4	27.1	11.9
	Sesarma spp.	3.4	0.6	3.6	1.3
Portunidae	*Portunus pelagicus*	1.6	0.5	1.8	0.7
	Thalamita stimpsoni	0.4		0.7	
Mictyridae	*Mictyrus longicarpus*		0.5		1.0
Xanthidae	*Heteropenape* sp.		0.5		0.5
(b) Reptant Decapoda					
Penaeidae		3.8	4.6	3.2	2.3
Palaemonidae	*Macrobrachium* sp.	1.1	0.3	1.0	0.2
Callianassidae	*Callianassa australiensis*	0.1	0.3	0.5	0.8
Alpheidae	*Alpheus edwardsii*	4.5	5.4	7.4	14.3
(c) Isopoda					
Sphaeromidae			1.9		3.1
(d) Amphipoda					
Talitridae		1.7	2.6	0.6	1.3
ANNELIDA		6.8	3.5	5.0	4.6
Capitellidae		2.4	1.0	1.1	0.8
Eunicidae		2.7	1.2	3.3	3.4
Nephtyidae		0.6	0.7	0.2	0.3
Oweniidae		1.1	0.5	0.4	0.2
MOLLUSCA		1.9	36.2	2.6	20.8
(a) Gastropoda					
Onchidaceae	*Onchidium* sp.	1.2	1.3	2.2	5.5
Naticidae	*Polinices sordidus*		1.1		0.1
Rissoidae	*Stenothyra* sp.		1.1		0.5
(b) Bivalvia					
Lucinidae		0.3	0.8	0.1	0.4
Tellinidae	*Macomona deltoidalis*	0.4	0.6	0.3	0.3
Glauconomidae	*Glaucomone virens*		32.3		13.9
PISCES		0.6	1.8	1.0	4.2
Gobiidae		0.6	1.8	1.0	4.2
PLANTS		3.8	7.9	2.1	1.4
UNIDENTIFIED MATERIAL		1.5	1.8	1.4	1.5

contrast, *S. sihama*, which occurred sympatrically with *S. analis* in the Townsville study, displayed a more delicate pharangeal dentition and was found to eat mainly soft bodied food types (Gunn and Milward, 1985). *S. analis* therefore appears capable of eating a wide variety of benthic animals. This may be a possible explanation for the variation in the diet of *S. analis* observed in three different Australian locations.

References

BALL, J. N., 1961. — On the food of the brown trout of Llyn Tegid. *Proc. Zool. Soc. Lond.* 137: 599-622.

GUNN, J. S., and MILWARD, N. E., 1985. — The food, feeding habits and feeding structures of the whiting species *Sillago sihama* (Forsskål) and *Sillago analis* Whitley from Townsville, North Queensland, Australia. *J. Fish. Biol.* 26: 411-427.

HYNES, H. B. N., 1950. — The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of methods used in studies of the food of fishes. *J. Anim. Ecol.* 19: 36-58.

LENNANTON, R. C. J., 1969. — Whiting fishery — Shark Bay. *Fishing Industry News Service* 2(1): 4-11. W. Aust. Dept Fish. Wildl.

McKAY, R. J, 1985. — A revision of the fishes of the family Sillaginidae. *Mem. Qld Mus.* 22(1): 1-73.

SIEGEL, S., 1956. — *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw Hill.

Communicated by J. R. Merrick; manuscript received 5 August 1986, accepted for publication 22 October 1986.

Notes and Discussion

PROCEEDINGS of LINNEAN SOCIETY OF NEW SOUTH WALES

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Issued 12th July, 1988

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Printed by Southwood Press Pty Limited,
80-92 Chapel Street, Marrickville 2204

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LINNEAN SOCIETY
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NEW SOUTH WALES

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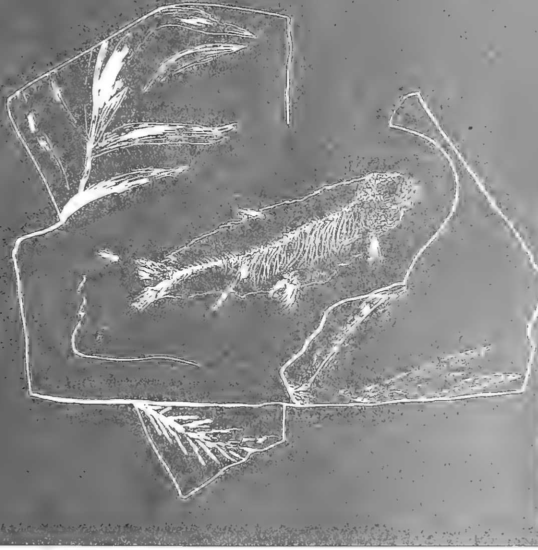

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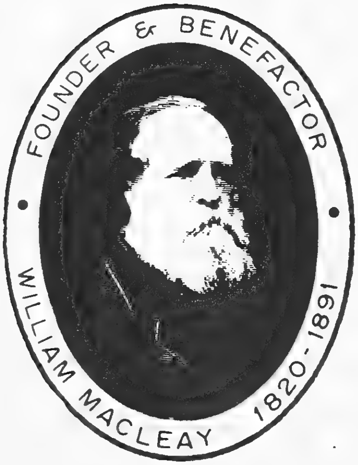

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PROCEEDINGS
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VOLUME 110
NUMBER 3

Fluxes of Inorganic Nitrogen between Sediments and Water in a Coral Reef Lagoon

R. JOHNSTONE*, K. KOOP and A. W. D. LARKUM

JOHNSTONE, R., KOOP, K., & LARKUM, A. W. D. Fluxes of inorganic nitrogen between sediments and water in a coral reef lagoon. *Proc. Linn. Soc. N.S.W.* 110 (3), (1988) 1989: 219-227.

Lagoon sediments of coral reefs are potentially important sites of nutrient regeneration. Profiles of ammonium within sediments at One Tree Island, southern Great Barrier Reef, showed strong gradients with values as high as 50μg atoms NH_4^+-N.l^{-1} at 15cm depth decreasing to around 8μg atoms.l^{-1} just below the surface. Gradients of NO_3^-/NO_2^- also existed but concentrations were much lower than for ammonium, ranging from undetectable levels to approx. 8μg atoms.l^{-1}. Overlying waters characteristically have low to undetectable levels of dissolved ammonium or nitrate/nitrite. Nutrient profiles were examined in the top 0-10cm of two sediment types and despite strong concentration gradients, no efflux of NH_4^+ ions or NO_3^-/NO_2^- ions were observed from the sediment into the water column. In experiments where the water under domes was artificially enriched with ammonium chloride to maximum sediment concentrations (50μg atoms NH_4^+-N.l^{-1}) rapid uptake of NH_4^+-N by sediments was shown to occur. Microbial processes such as nitrification, denitrification, and ammonium utilization by psammolithic algae in the uppermost layers of sediment may be responsible for the observed phenomena.

R. Johnstone and A. W. D. Larkum, School of Biological Sciences, University of Sydney, Sydney, Australia 2006, and K. Koop, Zoology Department, Stockholm University, S-106 91, Stockholm, Sweden; (R. Johnstone, present address, *Zoology Department, Stockholm University, S-106 91, Stockholm, Sweden); *manuscript received 17 March 1987, accepted for publication 23 March 1988.*

INTRODUCTION

Since the pioneering work of Odum and Odum (1955), Wiebe *et al.* (1975), and Webb *et al.* (1975), different aspects of nitrogen dynamics on coral reef ecosystems have been investigated (e.g. Wiebe, 1976; Smith and Jokiel, 1975; Webb and Wiebe, 1975; Capone *et al.*, 1975; Hatcher and Hatcher, 1981; and Koop and Larkum, 1987). Apart from the work of Entsch *et al.* (1983) and Williams *et al.* (1985), however, there are few published studies on nitrogen cycling in coral reef sediments, although many such studies exist for other environments (see e.g. Raine and Patching, 1980; Hopkinson and Wetzel, 1982).

Nitrogen fixation is widely believed to be responsible for supplying large amounts of nitrogen to coral reef ecosystems (Webb *et al.*, 1975; Wilkinson *et al.*, 1984; and others) although Koop and Larkum (1988) have shown that only 10-15% of nitrogen requirements of primary producers at One Tree Island, southern Great Barrier Reef, can be met by direct nitrogen fixation. There is still a substantial deficit which must be met from other sources such as remineralization by microorganisms.

This study assesses the role of sediments as a source of recycled nitrogen for the adjacent systems by measuring levels of ammonium, nitrate and nitrite within sediments as well as fluxes of these ions between sediments and the overlying water column in One Tree Is. lagoon, southern Great Barrier Reef.

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* *Formerly*, Linnean Macleay Fellow.

MATERIALS AND METHODS

Sites

The whole of this work was conducted in the main lagoon on One Tree Island Reef, Great Barrier Reef, Australia (lat. 20°30′S, long. 152°06′E), (Fig. 1) during summer, 1984.

Nutrient fluxes were measured in the two sediment types representing the range in sediment environments found in One Tree Is. lagoon. These were very fine sand and coarse sand with $>40\%$ of particles $<63\mu m$ diameter and $>40\%$ of particles $>1mm$ diameter respectively.

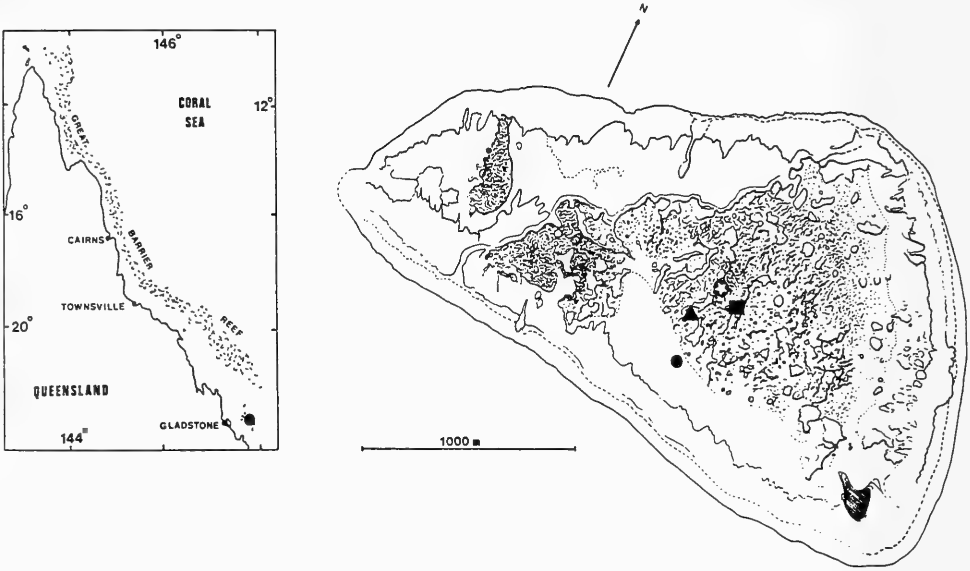

Fig. 1. One Tree Island reef, southern Great Barrier Reef showing (**B**, right) experimental sites in two sediment types.

● Coarse sand; ★ Very fine sand.

Mean water depth was 4.5m at the site with very fine sand and 1.5m at the site with coarse sand. All sediments in One Tree lagoon contain approx. 97% calcium carbonate, derived from the fringing and patch reefs.

Pore Water Sampling and Analysis

Four replicate cores 5cm diameter and 20cm deep, were taken randomly in areas of each sediment type and subsamples of $10cm^3$ were taken at depths of 0.5, 2.5, 5.0, 10.0 and 15.0cm from each core. The pore water from each subsample was extracted by centrifugation at 3,000 × g for 10 minutes and the concentration of ammonium, nitrate and nitrite ions determined according to Strickland and Parsons (1972). All analyses were conducted within 2 hours of core collection. Nitrate and nitrite analysis was conducted using a Technicon auto-analyser, model AA1.

Rates of efflux of NH_4^+ from the sediments were calculated using the equations of Rutgers van der Loeff *et al.*, (1984):

$$J = \phi D_s.dC/dx \qquad (\textit{Equation } 1)$$

where J = rate of flux,
ϕ = sediment porosity,
D_s = effective diffusion coefficient,
dC/dx = concentration gradient across the sediment/water interface.

Measurement of Sediment Fluxes

Measurement of fluxes of ions from the sediment were carried out using six polycarbonate domes placed randomly over the sediment at each site. The domes had a volume of 36 litres with a basal area of 640cm^2 and were anchored to a steel skirt pushed 5cm into the sediment. The skirt also served to prevent lateral movement of water under the edge of the domes.

In each dome, water above the sediment was sampled every 2 hours for 18 hours, using a 20ml syringe and needle pushed through a self-sealing sampling port on the side of the dome. An equal amount of seawater was allowed to enter the dome during sampling to prevent water being drawn from the sediment itself.

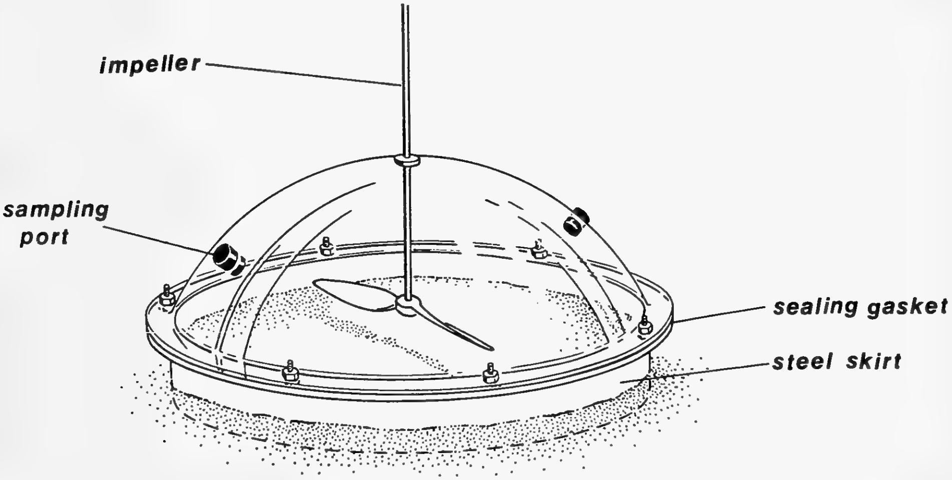

Fig. 2. Dome enclosures used for flux measurements and enrichment experiments showing hand driven impeller, sampling ports and anchoring base.

The water inside each dome was stirred with a hand-driven impeller mounted in its centre (Fig. 2) for 5 minutes every hour, and just prior to sampling. Care was taken to ensure that the stirring rate was low enough to leave the sediment undisturbed, but strong enough to ensure thorough mixing of the dome water.

Samples were immediately refrigerated for transport to the laboratory and analysis for ammonium, nitrate and nitrite ions was carried out within 5 hours of collection as for pore-water samples.

Enrichment Experiments

In experiments using four replicate domes placed randomly over the sediment at each site, the water under the domes was enriched with ammonium chloride to produce a concentration of dissolved ammonium ions approximately equal to the maximum concentration found in the underlying sediment. Four control domes were also set up at each site with no enrichment. Water in all domes and their immediate surrounds was sampled every 2 hours for 17 hours and the samples analysed for ammonium concentration, oxygen concentration, pH, and temperature.

Also, as a control for uptake of ammonium by organisms in the water column, twelve 500ml bottles, 6 light-proof and 6 transparent, were filled with seawater taken at each site and enriched with ammonium chloride to the same concentration as the enriched domes. Controls were incubated *in situ* for the duration of the enrichment experiment and sampled at the start, midway, and at the end of the experiment. The samples were analysed for dissolved ammonium as before.

Temperature and dissolved oxygen were measured *in situ* with a submersible combination temperature/oxygen probe attached to a YSI meter (model number 57; Yellow Springs Instruments, Ohio, U.S.A.). Sample pH was determined immediately after collection with an Activon 105 portable pH meter.

The expected flux rates of ammonium ions from the enriched dome water into the underlying sediment were calculated with the Stokes-Einstein equation for diffusion (Crank *et al.*, 1981):

$$C = M/2.(\pi Dt)^{-1/2}.\exp(-r^2/4Dt) \qquad \text{(\textit{Equation} 2)}$$

where C = concentration of solute,
M = quantity of solute emitted at $t=O$ from unit area of the plane of origin,
D = the diffusion coefficient,
t = time,
r = the distance of the point of measurement from the plane of source.

This equation describes the decrease of a solute with time due to simple diffusion. By considering the underlying sediment as an infinite sink the equation would give the maximum rate of diffusion possible and enable us to speculate on the possibility of active uptake by sediment or water column organisms.

RESULTS

Pore-Water Ammonium, Nitrate/Nitrite, and Sediment-Water Column Fluxes

Both sediment types showed the same concentration of free ammonium at 15cm depth (38μg atoms $NH_4{}^+$-N.l^{-1}) but above this depth the concentration gradients were considerably different (Fig. 3). In the very fine sand site the concentration had a pronounced peak at 5cm depth (50μg atoms $NH_4{}^+$-N.l^{-1}) with the lowest concentration in the top 1cm of sediment (18μg atoms NH_4t-N.l^{-1}). By comparison the coarse sand site showed a peak ammonium concentration at 15cm depth (38μg atoms $NH_4{}^+$-N.l^{-1}), with a gradual decrease toward the top 1cm of sediment (8μg atoms $NH_4{}^+$-N.l^{-1}), (Fig. 3). Nitrate/nitrite concentration gradients for both sediment types showed a small peak just below the sediment surface; 6.75 ± 8.8μg atoms $NO_3{}^-/NO_2{}^-$-N.l^{-1} (n=4) at 5cm in the coarse sand and 7.0 ± 7.8μg atoms $NO_3{}^-/NO_2{}^-$-N.l^{-1} (n=4) at 2.5cm in the very fine sand (Fig. 4). In both sediment types, $NO_3{}^-/NO_2{}^-$ concentrations decreased with increasing sediment depth and concentrations were usually barely above detection limits.

Despite the existence of reasonably strong concentration gradients of $NH_4{}^+$ and the occurrence of measurable amounts of $NO_3{}^-/NO_2{}^-$ in the sediments at One Tree Is., no flux of dissolved $NH_4{}^+$ or $NO_3{}^-/NO_2{}^-$ into the overlying water column was observed from either type of sediment studied. Also no dissolved ammonium was detected in the surrounding seawater at the site with coarse sand, but water at the site with very fine sand consistently had an $NH_4{}^+$ concentration of 1.9 ± 0.1μmols.l^{-1}. $NO_3{}^-/NO_2{}^-$ ions were undetectable in the surrounding water over both study sites.

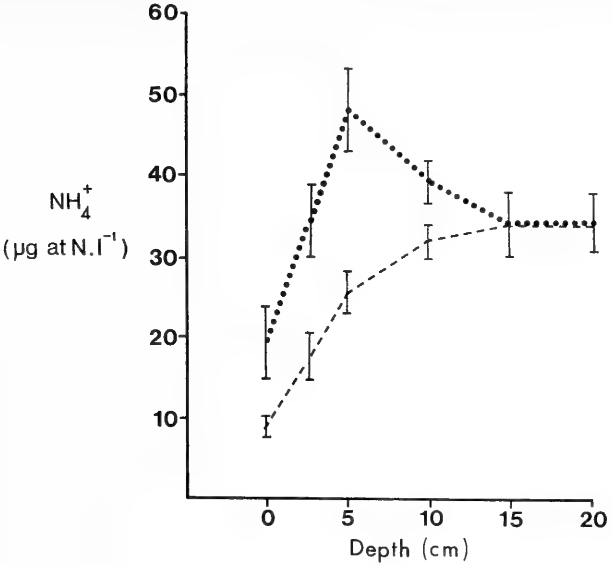

Fig. 3. Concentration gradients of ammonium in pore-water of two sediment types at One Tree Is. Vertical bars are 95% confidence limits (n = 4).
●●●●●● Very fine sand; – – – – – Coarse sand.

Using the concentration gradients from the top 5cm of each sediment type the expected rates of $NH_4{}^+$ efflux from the sediment surface were calculated with the Stokes-Einstein equation. This was corrected for temperature variation and used a diffusion coefficient of $19.8 \times 10^{-6}cm^2.s^{-1}$ (Li and Gregory, 1974). The resulting flux rates were 2.55µg atoms $N.m^{-2}.h^{-1}$ for coarse sand, and 1.85µg atoms $N.m^{-2}.h^{-1}$ for the very fine sand.

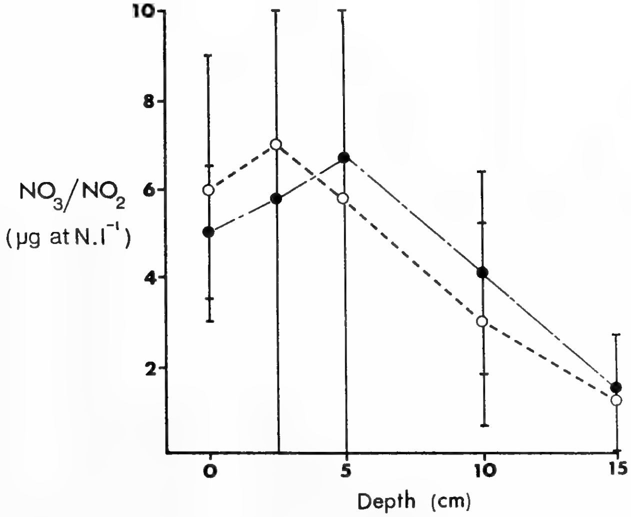

Fig. 4. Concentration gradients of nitrate/nitrite in pore-water of two sediment types at One Tree Is. Vertical bars are 95% confidence limits (n = 4).
○– – – –○ Very fine sand; ●—— – ——● Coarse sand.

Enrichment Experiments

Experiments in sites with both the very fine sand and coarse sand showed approximately exponential loss of NH_4^+ over the experimental period (Fig. 5**A**,**B**). Above the very fine sand the rate of loss showed a short but distinct plateau centred on the time of total dark, approximately 7.5 hours after the start of the experiment. The plateau lasted approximately 4 hours and was followed by a slower rate of decrease in NH_4^+ ions than previously observed. Above the coarse sand there was no plateau, and the decrease in ammonium ion concentration over time was approximately exponential (Fig. 5**B**).

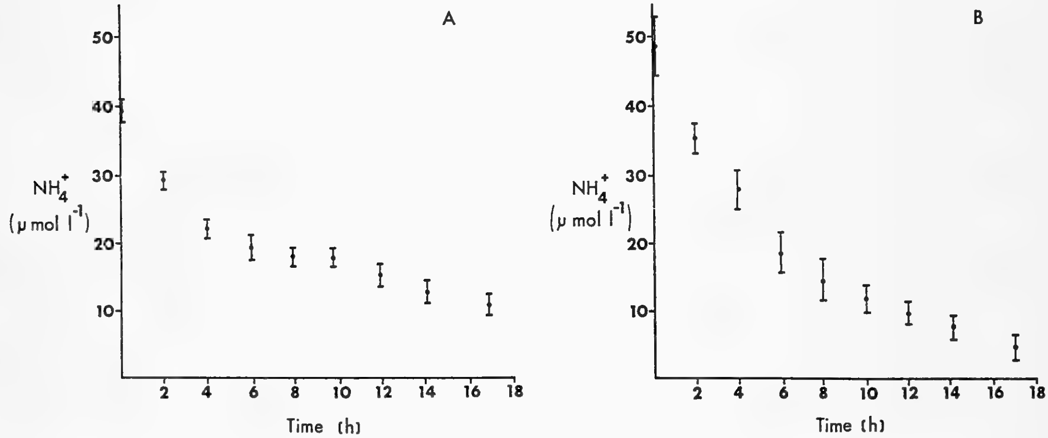

Fig. 5. Concentrations of ammonium in enriched dome water over very fine sand (**A**), and coarse sand (**B**) at One Tree Is. Note the plateau between 6 and 10 hours at the very fine sand site. Total dark occurred at 7 hours for both experiments. Vertical bars are 95% confidence limits (n = 4).

Using the Stokes-Einstein equation for diffusion, the calculated concentrations of ammonium ions in the water under the domes after 17 hours would be $10\mu M\ NH_4^+$ and $12\mu M\ NH_4^+$ for very fine and coarse sands respectively (this assumes diffusion at the sediment surface into an infinite sink for NH_4^+). The concentrations observed after 17 hours were $10 \pm 2\mu M$ for very fine sand and $5 \pm 2.5\mu M$ for coarse sand. These values are equal to or less than those calculated, indicating that the ammonium ions were being taken up at near maximal rates.

At the end of the experimental period, there was no significant difference between individual domes in the two types of sediments, or between treatments, for mean values of pH, temperature or dissolved oxygen in the water enclosed by the domes, and there was no difference between entrapped dome water and unenclosed water for these parameters (Table 1). Also, there was no decrease in the concentration of ammonium ions in the control bottles of enriched water incubated over the 17 hour period indicating that there was no detectable uptake of ammonium ions by water column organisms.

DISCUSSION

Physical variations, such as grain size, have received little attention in relation to nutrient levels in sediments of coral reefs (e.g. Entsch *et al.*, 1983). We have shown here (Fig. 3) that the ammonium concentration in the first 15cm of sediment is higher in the fine compared to the coarse sediment. Although many factors may be involved in determining these gradients, it is likely that differences in the metabolic activity of microbial populations of each sediment type varies the nutrient levels. This conclusion is

TABLE 1

Mean values and standard deviations of dissolved oxygen, pH, and temperature in enriched dome water, control dome water, and surrounding seawater over the two study sites for enrichment experiments January, 1985

		O_2 (ppm)	pH	Temperature (°C)
Very Fine Sand.	Enriched	5.93 ± 1.21	8.03 ± 0.09	28.25 ± 0.82
	Control	5.82 ± 1.23	8.06 ± 0.10	28.25 ±0.86
	Seawater	6.17 ± 0.73	8.08 ± 0.18	28.57 ± 0.90
Coarse Sand.	Enriched	7.37 ± 1.67	8.01 ± 0.18	27.88 ± 1.16
	Control	6.87 ± 2.00	7.99 ± 0.18	27.95 ± 1.24
	Seawater	6.20 ± 1.51	7.96 ± 0.14	28.00 ± 1.45

consistent with work elsewhere that shows grain size and porosity influence the nutrient levels of sediments, and are correlated with changes in sediment microbial and invertebrate populations (Dale, 1974; Jansson, 1967).

The concentration gradients from NO_3^-/NO_2^- observed here are similar to those found in coral reef sediments elsewhere (Corredor and Morell, 1985) and the concentrations found at One Tree Is. fall in the same range as found in sediments on the northern Great Barrier Reef (Boon, 1986). We suggest that the peak in NO_3^-/NO_2^- concentrations close to the sediment surface is due to bacterial nitrification which has been shown in other types of marine sediment to occur in the oxygenated zone (e.g. Henriksen, 1980; Henriksen *et al.*, 1981). Ammonium needed for this process would be supplied from the deeper anoxic zones where ammonification occurs and the concentration gradients observed here are more than adequate for this process. The absence of a NO_3^-/NO_2^- flux from the sediments into the water column is consistent with work on fluxes by Harrison (1983), who found that they were mostly negative (i.e. from the water column into the sediment). It is likely that the NO_3^-/NO_2^- pool, which is small compared with the ammonium pool is either utilized as a nitrogen source, or used in denitrification by the microbial population in the top layers of sediment.

For dissolved ammonium, concentration gradients and pools were up to an order of magnitude higher than for NO_3^-/NO_2^-. Despite the relatively steep concentration gradients of dissolved ammonium ions, and although an efflux of NH_4^+ ions has been observed elsewhere for coral reef sediments (Williams *et al.*, 1985), no efflux of ammonium ions from the sediment into the water column was observed in this study. Using the NH_4^+ concentration gradients in the One Tree reef sediments, and assuming a passive system, there should be a theoretical flux of NH_4^+ ions out of the sediment of 2.55μmols NH_4^+-N.m^{-2}.h^{-1}, for coarse sand; and 1.85μmols NH_4^+-N.m^{-1}.h^{-1}, for very fine sand.

The fact that no such flux was observed indicates that an active uptake process must be occurring in the top layers of sediment and this is substantiated by the fact that when the water under the domes was enriched with ammonium ions, its concentration decreased over time despite an opposing concentration gradient in the underlying sediments. Applying the Stokes-Einstein equation for diffusion (Crank *et al.*, 1981) of ammonium ions out of the domes and into the sediment, it is possible to show that ammonium was leaving the dome at near maximum rates (assuming a diffusive process). Ammonium ions are not used by organisms in the water column as shown by the bottle experiments, thus it is concluded that the ammonium is rapidly taken up and used, or modified, by organisms in or on the top layers of sediment; despite the fact that these organisms are also receiving a flux of ammonium ions from deeper sediments.

Use of free ammonium ions by marine microalgae is well known (e.g. Syrett, 1953; Goldman and Glibert, 1982) and microscopic inspection of water from the enriched domes and the top 1cm of sediment showed a suite of microalgae to be present in the sediment, but only rarely present in water samples. Thus microalgae may at least in part be responsible for the uptake of ammonium from the sediment but as indicated above other processes such as nitrification and denitrification may also change ammonium concentrations. Because of the size of the ammonium pool in One Tree reef sediments, however, it is unlikely that it could all be processed via nitrification and subsequent denitrification. If this were the case, then the corresponding denitrification rate would be approximately 2.4μmols $N_2O.m^{-2}.h^{-1}$. This is almost ten times the rate observed by Seitzinger and D'Elia (1985) for coral reef sediments (0.3μmols $N_2O.m^{-2}.h^{-1}$), and comparable to rates found in marine sediments with a much higher organic input (Nishio *et al.*, 1983). The level of nitrification and denitrification in One Tree reef sediments is presently being studied.

Apart from microbial composition, other biological factors likely to affect sediment nutrient levels are bioturbation and grazing which occur in surface layers. Both types of sediment discussed here are disturbed by burrowing shrimps and deposit feeding organisms such as holothuria. Such organisms significantly affect bacteria in sediments (Juniper, 1981). At One Tree reef, most turbating organisms were observed in the top 15cm of sediment where the concentration gradients between the two sediment types are most different.

In addition, the coarse sand is often exposed to currents which can totally rework the top 5 to 10cm of sediment (Frith, 1985). Although such currents were not observed during the period of this study, they occur fairly frequently. Combined with the activities of turbating organisms such currents probably affect the incorporation of organic matter into, and general stability of the sediment.

In summary these results show that the sediments at One Tree reef do not release free dissolved ammonium, nitrate or nitrite ions for use by primary producers or other organisms in the water column or hard substrate communities, but appear to contain microorganisms capable of using and modifying this nitrogen. Presumably nitrogen ultimately leaves the sediments in forms other than dissolved ions possibly via grazers of micro-organisms, but the processes involved are still to be identified.

ACKNOWLEDGEMENTS

We thank Philip Smith and Penny Butcher, managers of One Tree Island field station, as well as Rod Smith for their support and assistance in the field. The study was supported by the award of a Linnean Macleay Fellowship and a Joyce Vickery research grant from the Linnean Society of N.S.W. to R. Johnstone, and an Australian Marine Science and Technologies grant to A. W. D. Larkum.

References

BOON, P. I., 1986. — Uptake and release of nitrogen compounds in coral reef and seagrass, *Thalassia hemprichii* (Ehrenb.) Aschers., bed sediments at Lizard Island, Queensland. *Aust. J. Mar. Freshw. Res.* 37: 11-19.

CAPONE, D. G., TAYLOR, D. L., and TAYLOR, B. F., 1975. — Nitrogen fixation associated with macroalgae in a coral reef community in the Bahamas. *Mar. Biol.* 40: 29-32.

CORREDOR, J. E., and MORELL, J., 1985. — Inorganic nitrogen in coral reef sediments. *Mar. Chem.* 16: 379-384.

CRANK, J., MCFARLANE, N. R., NEWBY, J. C., PATERSON, G. D., and PEDLEY, J. B., 1981. — *Diffusion Processes in Environmental Systems*. London: Macmillan Press Ltd.

DALE, N. G., 1974. — Bacteria in intertidal sediments: Factors related to their distribution. *Limnol. Oceanogr.* 19: 509-518.

ENTSCH, B., BOTO, K. G., SIM, R. G., and WELLINGTON, J. T., 1983. — Phosphorus and nitrogen in coral reef sediments. *Limnol. Oceanogr.* 28: 465-476.

FRITH, C. A., 1985. — Lagoon circulation at One Tree Reef, Southern Great Barrier Reef. Sydney: University of Sydney, Ph.D. thesis, unpublished.

GOLDMAN, J. C., and GLIBERT, P. M., 1982. — Comparative rapid ammonium uptake by four species of marine phytoplankton. *Limnol. Oceanogr.* 27: 814-828.

HARRISON, J. T., 1983. — Metabolism of interreef sediment communities. *NOAA Symposia Series for Undersea Research.* 1: 145-149.

HATCHER, B. G., and HATCHER, A. I., 1981. — Seasonal and spatial variation in dissolved inorganic nitrogen in One Tree Is. Lagoon. *Proc. 4th Int. Coral Reef Symp.* 1: 419-424.

HENRIKSEN, K., 1980. — Measurement of in situ rates of nitrification in sediment. *Microb. Ecol.* 6: 329-337.

——, RASMUSSEN, B., and JENSEN, A., 1983. — Effect of bioturbation on microbial nitrogen transformation in the sediment and fluxes of ammonium and nitrate to the overlying water. *Ecol. Bull.* 35: 193-205.

HOPKINSON, C. S., and WETZEL, R. L., 1982. — In situ measurements of nutrient and oxygen fluxes in a coastal marine benthic community. *Mar. Ecol. Prog. Ser.* 10: 29-35.

JANSSON, B., 1967. — The significance of grain size and pore-water content for the interstitial fauna of sandy beaches. *OIKOS* 18: 311-322.

JUNIPER, S. K., 1981. — Stimulation of bacterial activity by a deposit feeder in two New Zealand intertidal inlets. *Bull. Mar. Sci.* 31(3): 691-701.

KOOP, K., and LARKUM, A. W. D., 1987. — Deposition of organic material in a coral reef lagoon, One Tree Is., Great Barrier Reef. Estuar. *Coastal Shelf Sci.* 25: 1-9.

——, and ——, 1988., — Quantitative significance of nitrogen fixation on a coral reef, One Tree Island, southern Great Barrier Reef. P.S.Z.N. 1. *Marine Ecology* (in press).

LI, Y.-H., and GREGORY, S., 1974. — Diffusion of ions in seawater and in deep-sea sediments. *Geochim. Cosmochim. Acta* 38: 703-714.

NISHIO, T., KOIKE, I., and HATTORI, A., 1983. — Estimates of denitrification and nitrification in coastal and estuarine sediments. *Appl. Environ. Microbiol.* 45: 444-450.

ODUM, H. T., and ODUM, E. P., 1955. — Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecol. Monogr.* 25: 291-320.

RAINE, R. C. T., and PATCHING, J. W., 1980. — Aspects of carbon and nitrogen cycling in a shallow marine environment. *J. Exp. Mar. Biol. Ecol.* 47: 127-139.

RUTGERS VAN DER LOEFF, M. M., ANDERSON, L. G., HALL, P. O., IVERFELDT, A., JOSEFSON, A. B., SUNDBY, B., and WESTERLUND, S. F. G., 1984. — The asphyxiation technique: An approach to distinguish between molecular diffusion and biologically mediated transport at the sediment-water interface. *Limnol. Oceanogr.* 29: 675-686.

SEITZINGER, S. P., and D'ELIA, P., 1985. — Preliminary studies of denitrification on a coral reef. *The Ecology of Coral Reefs.* REAKA, M. L. (ed.). NOAA Undersea Res. Ser.

SMITH, S. V., and JOKIEL, P. L., 1975. — Water composition and biogeochemical gradients in the Canton Atoll lagoon: 2). Budgets of phosphorous, nitrogen, carbon dioxide and particulate material. *Mar. Sci. Comm.* 1: 162-207.

STRICKLAND, J. D. H., and PARSONS, T. R., 1972. — A practical handbook of seawater analysis (2nd ed.). *Fish. Res. Bd. Can. Bull.* 167.

SYRETT, P. J., 1953. — The assimilation of ammonia by nitrogen starved cells of *Chlorella vulgaris. Ann. Bot.* (Lond.) 65: 1-19.

WEBB, K. L., and WIEBE, W. J., 1975. — Nitrification on a coral reef. *Can. J. Microbiol.* 21: 1427-1431.

——, DUPAUL, W. D., WIEBE, W. J., SOTTILE, W., and JOHANNES, R. E., 1975. — Enewetok Atoll: Aspects of the nitrogen cycle on a coral reef. *Limnol. Oceanogr.* 20: 198-210.

WIEBE, W. J., 1976. — Nitrogen cycle on a coral reef. *Micronesia* 12: 23-26.

——, JOHANNES, R. E., and WEBB, K. L., 1975. — Nitrogen fixation in a coral reef community. *Science* 188: 257-259.

WILKINSON, C. R., WILLIAMS, D. MCB., SAMMARCO, P. W., HOGG, R. W., and TROTT, L. A., 1984. — Rates of nitrogen fixation on coral reefs across the continental shelf of the central Great Barrier Reef. *Mar. Biol.* 80: 255-262.

WILLIAMS, S. L., GILL, I. P., and YARISH, S. H., 1985. — Nitrogen cycling in backreef sediments; St. Croix, U.S. Virgin Is. *Proc. 5th Int. Coral Reef Congress*, Tahiti. 3: 389-394.

Estuarine Foraminiferal Communities in Lake Illawarra, N.S.W.

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YASSINI, I., & JONES, B. G. Estuarine foraminiferal communities in Lake Illawarra, N.S.W. *Proc. Linn. Soc. N.S.W.* 110 (3), (1988) 1989: 229-266.

Lake Illawarra is a shallow brackish coastal lagoon which formed behind a marine sand barrier following the last rise in ocean level. It is connected to the ocean by an active tidal channel. Tidal flushing of the lagoon is slow and it ranges in salinity from 16°/oo to 40°/oo. The lagoon is rapidly filling with sand and silt, with the sand mainly confined to banks around the lagoon margins. The substrate and turbidity of the lagoon control the distribution of floral communities which, in turn, influence the benthic invertebrates.

The distribution and composition of estuarine foraminiferal communities in Lake Illawarra depend on salinity, substrate and the rate of tidal exchange. In semi-enclosed estuarine lagoons the diversity of foraminiferal assemblages shows a marked decrease from the open ocean to the body of the lagoon. The connecting channel between the lagoon and the ocean is subject to diurnal tidal flushing and it contains a mixed assemblage of reworked and living intertidal and subtidal species with minor contributions of lagoonal species. The assemblage in the mobile sands of the tidal channel is much lower than on the seagrass-covered banks of the channel. Within the main body of the lagoon, where salinity is slightly lower than in the open ocean and tidal exchange is minor, foraminiferal assemblages are controlled by the substrate and its associated floral constituents. The sandy sediments around the margin of the lagoon have a foraminiferal assemblage characterized by a range of textulariinid species whereas the deeper and silty portions of the lagoon are dominated by two species of rotaliinids. *Ammonia beccarii* is an environmentally-tolerant species occurring at almost all the lagoonal to intertidal marine sample sites. Foraminifer population densities in the lagoon range from high to very low or absent depending on the quantity of available oxygen at the sediment-water interface.

In New South Wales, lagoonal foraminiferal communities differ significantly from communities developed in more open estuaries where tidal exchange is rapid. In the latter foraminiferal communities are more diverse and depend largely on the substrate and water depth, with salinity variations only affecting populations in the upstream portions of the estuary.

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INTRODUCTION

The distribution of foraminifers in Lake Illawarra, a coastal lagoon located 80km south of Sydney in New South Wales, has been determined from 132 samples collected from the lagoon, its tidal entrance channel and the adjacent marine intertidal Windang Island. The purpose of this study is to describe the faunal composition and distribution patterns of the foraminifers in the lagoon and adjacent upper intertidal environments.

Foraminiferal assemblages have been described from a number of bays, estuaries and lagoons along the coast of New South Wales (e.g., Albani, 1968, 1978, 1979, 1981; Albani and Johnson, 1976; Cotter, 1980) and from other Australian coastal environments (e.g., Apthorpe, 1980; Cann and Gostin, 1985; Collins 1958, 1974; Parr, 1932, 1945; Quilty, 1976). In addition, a number of studies have provided information about the physical parameters and seagrass communities in N.S.W. estuarine environments (e.g., Anderson and Story, 1981; Anderson *et al.*, 1981; Eliot *et al.*, 1976; Harris 1976a, b; Jones *et al.*, 1976; Public Works Department, 1985; Roy and Peat, 1975; Yassini and Wright, 1988) which can be related to their foraminiferal assemblages and thus provide a basis for erecting general foraminiferal biotope models for coastal environments.

PHYSICAL CHARACTER OF LAKE ILLAWARRA

A recent appraisal of the physical and chemical character of Lake Illawarra has been given in Yassini and Jones (1987). Lake Illawarra is a shallow elongate coastal lagoon situated 80km south of Sydney, N.S.W. It covers an area of about 34km^2 (Fig. 1) and fills a coastal depression scoured into the Late Permian Shoalhaven Group.

Fig. 1. Sample locations, water depths (in metres) and the distribution of sand-dominated substrates in Lake Illawarra.

The lagoon was formed during the last rise in ocean level some 6000-6500 years ago by the formation of a marine sand barrier north and south of Windang Island which impounded and flooded the former shallow marine embayment. The lagoon has a maximum depth of about 3.7m and an average depth of 1.9m (Roy and Peat, 1975). At present the lagoon water level is about 25-30cm above the mean ocean level and it is separated from the ocean by a tidal channel 2.4km long, approximately 600m wide and up to 3.5m deep. The seaward end of the channel is continuously changing its position and shape, and heavy shoaling of the mouth occasionally causes complete closure of the lagoon.

Lake Illawarra has an average annual fresh water input of about 80 × $10^6 m^3$ (Ellis *et al.*, 1977). The tidal range along the landward margins of the lagoon is about 3-5cm increasing to 10-25cm near the tidal entrance channel. The average tidal exchange between the lagoon and the ocean is about 0.5 × $10^6 m^3$ giving a residence time of approximately 26-39 weeks for the lake water mass (Ellis *et al.*, 1977). Tidal currents are essentially limited to the entrance channel and currents within Lake Illawarra are mainly wind generated (Clarke and Eliot, 1984).

The average monthly lagoon surface water temperature ranges from 9°C in June to 29°C in February. At most times there is no significant difference between the surface and bottom water temperatures in the lagoon.

Sandy sediments within Lake Illawarra are confined to water depths shallower than 2m and they are most abundant along the eastern margin of the lake and around the Macquarie Rivulet and Mullet Creek deltas (Fig. 1). The central part of the lagoon has low relief with a depth of 2m to 3.7m and the sediments consist of dark grey silt and clay containing volatile organic matter (15-19%), iron monosulphides and faecal pellets.

CHEMICAL CHARACTERISTICS OF LAKE ILLAWARRA

The salinity of the lagoon ranges from 16‰ to 40‰ depending on the balance between fresh water inflow, evaporation and the rate of tidal exchange. The salinity is within the normal estuarine range and, except during flood periods, low salinities are confined to stream mouths. Throughout the main body of the lagoon there is very little lateral or vertical variation in salinity values (<3‰, Ellis *et al.*, 1977) due to wind induced circulation and mixing of the water.

The mean pH of the surface layer in the lagoon varies between 7.3-8.3. In late winter, spring and summer, blooms of macro-algae increase the surface pH to almost 10 during the day but it returns to 7.3 at night. However, just below the water-sediment interface the connate water may be slightly acidic.

According to Ellis and Kanamori (1977) and the Electricity Commission of New South Wales (1982-1983) the concentration of dissolved oxygen in the surface layer of the lagoon during the day varies between 4-11mg/l. However, large fluctuations in dissolved oxygen concentrations between night and day occur in areas on the eastern side of the lagoon affected by algal blooms. For example, during one bloom in Griffins Bay the dissolved oxygen content ranged from a daytime maximum of 14mg/l to a night-time minimum of 1.5mg/l, with only 0.5mg/l of dissolved oxygen at the water-sediment interface. Salinity stratification and oxygen depletion of the bottom layer often occur after major flooding and periods of heavy rain (Gibbs, 1986). Nocturnal oxygen deficiencies are important in pH-Eh-related reactions in the bottom sediments, especially in the release of phosphorus to the water column and the denitrification of nitrate and nitrite.

As an enclosed saline coastal lagoon, with very limited tidal exchange and almost entirely surrounded by residential and industrial development, Lake Illawarra is subjected to continuous pollution. The pollutants are of three major categories: suspended solids, excess nutrients and heavy metals.

Suspended solids consist mainly of silt and clay which are removed from the catchment by erosion, especially river bank collapse, and are washed out of urban centres bringing some $100,000 m^3$ of sediments annually into the lagoon. This can rise to $270,000 m^3$ in years with major floods (Hean and Nanson, 1985). Flood tidal currents bring an annual average 110,00m^3 of marine sand (Public Works Department, N.S.W., 1985) into the lagoon through the entrance channel. Fly-ash particles from Tallawarra Power Station (1952-present) and Port Kembla (1928-present) are also abundant in the lagoon sediments (Jones *et al.*, 1976). Coal-wash and slag deposited as back-fill in the lagoon catchment area have also contributed to the solid pollutants in the lagoon. Suspended solids increase turbidity, inhibit photosynthetic processes and increase the rapid infilling of the lagoon. The mean turbidity level of the lake for the period 1984-1985 was 6NTU.

Rural and urban drainage networks contribute large quantities of nitrogenous and phosphatic leachates to the lagoon and its bottom sediment and these contribute to the excess growth of macro-algae. During June 1985 an algal bloom produced 71,000 tonnes of macro-algae (Yassini, in prep.) and the subsequent decomposition of this mass caused an oxygen deficiency at the sediment-water interface allowing the production of H_2S and black iron monosulphides.

High localized concentrations of heavy metals in the top 25cm of lagoon sediments have been recorded by Jones *et al.* (1976), Roy and Peat (1975) and Ellis and Kanamori (1977). The main pollutants are zinc, lead and cadmium which were probably derived from the Dapto Smelting Works (1895-1906) and the Port Kembla industrial complex since 1928.

BENTHIC FLORA AND FAUNA IN LAKE ILLAWARRA

Both angiosperms and algae are important benthic floral constituents in the lagoon but are confined to water depths shallower than 2m since the high turbidity restricts light penetration to greater depths. On the shallow water sandy and muddy sandbanks along the tidal entrance channel and Windang Peninsula, around Mullet Creek and Macquarie Rivulet deltas and in Griffins and Koona bays four species of aquatic angiosperm (*Ruppia megacarpa* Masson, *Zostera capricorni* Aschers., *Halophila decipiens* Ostenfeld and *Halophila ovalis* (R.Br.) Hook. f.) are abundant. They are associated with green, red and brown algae, and several species of epiphytic blue-green and red algae occur on the leaves of *Zostera* and *Ruppia*. On rocky outcrops along the northern, western and southern shores of Lake Illawarra brown, green and red algae are the dominant floral constituents. Details of the algal flora are given in Yassini and Jones (1987).

The benthic invertebrate fauna in Lake Illawarra displays a low diversity but a high population density which is typical of estuarine systems. Polychaete worms and the molluscs *Tellina (Macoma) deltoidalis* (Lamarck), *Spisula trigonella* (Lamarck) and *Hydrobia buccinoides* (Hedley) form over 90% of macrobenthic biomass. Other constituents include additional molluscs, amphipods, isopods, cirripedes, ostracods, decapods, reptantes and tubellarids.

FORAMINIFERS

For each of the 132 samples used in this study about 100cc of sediment was wet-sieved on a 200-mesh screen and the foraminifers were collected from 50cc of the washed residue, using conventional micro-palaeontological techniques. The foraminifers were not stained for live specimens since 2/3 of the samples came from a previous study (Jones *et al.*, 1976). The foraminifer classification (Appendix) used in this study conforms mainly to that of Loeblich and Tappan (1964, 1974, 1984). Additional references which were very useful for the specific identification of these southeastern Australian foraminifers include Albani (1974), Barker (1960), Brady (1884), Chapman and Parr (1937), Cushman (1932, 1933, 1942), Hermelin and Scott (1985), Kohl (1985), Matoba (1970), McCulloch (1977, 1981), Murray (1975), Poag (1981), Seibold (1975) and Sidebottom (1912, 1913).

A total of 123 benthonic and 6 planktonic foraminiferal species have been recognized in Lake Illawarra, its tidal entrance channel and the intertidal zone surrounding Windang Island. All the benthonic species are shallow water forms and the vast majority of these species have been recorded from the diverse populations at Windang Island (85 species) and the entrance channel to the lagoon (89 species). Within Lake Illawarra 16 species have been recorded, mainly from the margins of the lagoon; only two species are common from the central part of the lagoon. Thirty nine samples from the lagoon and entrance channel contained no foraminifers. Distribution of all identified species is summarized in Tables 1 to 3 and in the Appendix. The total benthonic foraminiferal population density is indicated in Fig. 2.

TABLE 1

Samples containing only Ammonia beccarii *and* Cribrononion sydneyensis

Ammonia beccarii only	239, Y23, Y26, Y29, Y34, Y36
Ammonia: Cribrononion ratio	
>10:1	77, 162, 467, Y24
10:1 to 5:1	340, 376, 386, Y6, Y7
5:1 to 2:1	161, 164, 166, 187, 198, 203, 220, 236, 342, 361, 373, Y1, Y2, Y4, Y9, Y12, Y21
2:1 to 1:1	21, 87, 142, 158, 159, 169, 181, 202, 234, 262, 265, 384, Y16, Y22, Y25, Y31, Y32, Y39
<1:1	85, 112, 310, 359

The foraminiferal population within the lagoon is dominated by two of the three species of rotaliinids with more restricted distributions for the two species of miliolinids and eleven species of textulariinids.

The rotaliinids form the most abundant group in the lagoon and are represented by *Ammonia beccarii* and *Cribrononion sydneyensis* (Tables 1 and 2). A comparison of Figs 1 and 3 indicates that the two dominant species of rotaliinids in the lagoon constitute the entire foraminiferal population throughout almost all the deeper parts of the lagoon and its shallow embayments where the substrate is muddy. *Cribrononion sydneyensis* is confined to the deeper water areas (Fig. 4) whereas *Ammonia beccarii* is a very tolerant species occurring in almost all foraminiferal assemblages from the lagoon (Table 1), tidal channel and intertidal environments. It dominates at water depths of less than 1m where the substrate is sandy but it decreases in relative abundance from the lagoon towards the open ocean.

Textulariinids are most abundant around Mullet Creek and Macquarie Rivulet deltas, Griffins Bay and the tidal entrance channel (Fig. 5). Agglutinated foraminifers were mainly observed on sandy substrates but in Griffins Bay they were present in clay-rich sediment. While there is no distinct areal zonation of textulariinid species through the lagoon there is a distinct difference between the lagoon and the entrance channel-marine assemblage. The textulariinid species confined to the lagoon include *Protoschista findens*, *Miliammina fusca*, *Ammobaculites agglutinans*, *A. foliaceus*, *Texturalia porrecta*, *Eggerella australis* and *Trochammina inflata*. *Tritaxis conica* occurs both in the northern half of the lake and in the entrance channel and marine assemblages.

Miliolinids have a very restricted distribution within the lagoon system and are confined essentially to the entrance channel, the shallow zone along Windang Peninsula and isolated occurrences around delta mouths (Fig. 6). The two species, *Triloculina oblonga* and *Miliolinella subrotunda*, were found on sandy substrates with dense to

TABLE 2

Foraminiferal abundance in sediments from the Lake Illawarra area
(% per 100cc sample)

	Miliammina fusca	*Protoschista findens*	*Reophax* sp.	*Ammobaculites agglutinans*	*Ammobaculites foliaceus*	*Ammobaculites* sp.	*Ammotium cassis*	*Tritaxis conica*	*Trochammina inflata*	*Textularia porrecta*	*Eggerella australis*	*Miliolinella subrotunda*	*Triloculina oblonga*	*Cribrononion sydneyensis*	*Ammonia beccarii*	*Rotalia perlucida*
16	–	–	–	–	–	–	–	–	5.9	–	–	–	–	76.5	17.6	–
36	–	–	–	–	–	–	–	–	–	–	–	–	33.3	–	66.7	–
41	–	–	–	–	27.3	–	–	63.6	–	–	–	–	–	–	9.1	–
102	4.3	4.3	–	–	87.0	–	–	–	–	–	4.4	–	–	–	–	–
108	–	–	–	–	–	–	–	33.3	–	–	–	–	–	33.3	33.3	–
138	–	–	–	–	0.4	–	–	0.9	–	–	26.8	–	–	–	71.4	–
206	–	–	–	5.1	–	–	–	–	–	–	–	–	–	44.3	50.6	–
245	6.3	2.1	–	–	2.1	–	–	–	83.3	–	–	–	–	–	–	6.3
306	9.9	12.4	–	–	43.2	–	–	–	24.7	–	–	–	–	2.5	4.9	2.5
334	–	–	–	–	92.9	–	–	–	–	–	–	7.1	–	–	–	–
363	–	–	–	–	3.3	–	–	–	–	–	–	–	–	30.0	66.7	–
379	–	1.0	–	–	1.0	–	–	–	–	–	–	–	–	40.6	57.3	–
390	–	–	–	–	–	–	–	–	–	–	–	–	14.7	85.3	–	–
393	–	2.9	–	2.9	–	–	–	–	–	–	–	–	–	13.3	80.9	–
408	–	–	–	–	–	–	–	–	–	–	–	0.4	–	42.4	57.2	–
Y10	–	16.7	–	–	–	11.1	–	27.8	5.6	–	22.2	–	–	–	16.7	–
Y13	–	3.2	3.2	1.3	–	–	–	2.0	–	16.1	16.1	–	–	12.9	45.2	–
Y15	–	–	–	–	12.5	–	–	–	–	–	–	–	–	–	87.5	–
Y28	–	–	–	–	19.4	–	–	–	–	–	–	38.7	–	–	41.9	–
Y30	–	–	–	–	–	–	0.8	–	–	2.3	19.2	–	–	0.8	76.9	–
Y33	1.4	–	–	–	–	–	–	1.4	–	–	–	–	27.8	–	69.4	–
Y37	–	–	–	–	–	–	–	–	–	–	–	37.5	–	25.0	37.5	–
K8	–	–	–	–	–	–	–	–	–	–	–	1.0	–	25.3	73.7	–

TABLE 3

Number frequency distribution of Foraminifera around Windang Island and in the entrance channel

	Entrance channel								Windang Island				
	59	273	282	297	Y18	Y19	Y20	Y39	Y41	Y42	Y44	Y46	Y52
Haplophragmoides canariensis	—	—	—	—	—	—	—	—	13	16	—	—	20
Tritaxis conica	—	—	4	—	—	5	—	2	2	—	—	—	—
Textularia candeiana	—	—	—	—	—	—	—	—	—	30	4	—	20
Textularia porrecta	—	—	1	—	—	—	—	—	—	—	—	—	—
Textularia sagittula	—	—	—	—	—	—	2	—	4	10	—	5	15
Textularia sp. I	—	—	—	—	—	—	—	—	—	—	—	—	4
Textularia sp. II	—	—	—	—	—	—	—	—	50	—	—	—	38
Eggerella subconica	—	—	—	—	—	—	—	—	2	—	—	—	28
Gaudryina convexa	—	—	—	—	1	—	1	—	—	5	—	—	13
Spiroluculina antillarum	—	—	—	—	—	—	—	—	10	—	—	—	14
Spiroloculina communis	—	—	—	—	—	—	5	—	—	—	—	—	3
Milliolinella baragwanathi	—	—	—	—	—	—	6	—	8	5	—	10	41
Milliolinella circularis	—	—	—	—	—	—	3	—	10	5	—	—	80
Milliolinella circularis subsp. nov.	—	—	—	—	—	—	—	—	—	—	—	—	6
Miliolinella subrotunda	—	—	1	—	—	—	—	—	—	1	—	—	—
Pyrgo subglobulus	—	—	—	—	—	2	—	—	—	—	—	—	1
Quinqueloculina granulocostata	—	—	—	—	—	—	—	—	1	—	—	—	—
Quinqueloculina poeyana	1	—	1	—	8	3	—	—	6	—	—	—	28
Quinqueloculina pseudoreticulata	—	—	—	—	—	2	—	—	8	5	3	—	8
Quinqueloculina seminula	—	—	4	—	—	—	—	—	—	—	—	—	36
Quinqueloculina subpolygona	—	—	—	—	—	15	10	—	10	10	3	52	184
Quinqueloculina tasmanica	—	—	—	—	—	—	—	—	2	—	—	—	—
Quinqueloculina tropicalis	—	—	—	—	—	—	—	—	3	—	—	—	5
Quinqueloculina sp. nov.	—	—	—	—	—	—	—	—	—	—	—	—	12
Triloculina oblonga	—	—	—	—	1	—	—	1	12	—	—	—	—
Triloculina tricarinata	—	—	—	—	—	—	—	—	1	—	—	—	—
Triloculina trigonula	—	—	—	—	1	—	4	—	—	10	10	—	34
Guttulina pacifica	—	—	1	—	—	5	—	—	—	—	—	—	8
Guttulina sp. I	—	—	—	—	—	—	—	—	—	3	—	—	—
Guttulina sp. II	—	—	—	—	—	1	—	—	—	—	—	—	1
Sigmoidella elegantissima	—	—	—	—	—	2	—	—	1	—	—	—	—
Amphicoryna scalaris	—	—	—	—	1	1	1	—	—	—	—	—	—
Bolivinella folia	—	—	—	—	—	1	—	—	—	—	—	—	—

TABLE 3 (continued)

	Entrance channel								Windang Island				
	59	273	282	297	Y18	Y19	Y20	Y39	Y41	Y42	Y44	Y46	Y52
Fissurina fasciata carinata	—	—	—	—	—	—	3	—	3	—	—	—	21
Fissurina lacunata	—	—	—	—	—	3	—	—	1	—	—	—	9
Fissurina marginatoperforata	—	—	—	—	—	1	—	—	—	—	—	—	—
Fissurina cf. *subquadrata*	—	—	—	—	—	—	—	—	—	—	—	—	2
Fissurina sulcata	—	—	—	—	—	1	—	—	—	—	—	—	—
Fissurina sp. I	—	—	1	—	—	—	—	—	—	—	—	—	—
Fissurina sp. II	—	—	—	—	—	1	—	—	—	—	—	—	—
Lagena acuticosta	—	—	—	—	—	—	—	—	—	—	—	—	1
Lagena crenata	—	—	1	—	—	—	—	—	—	—	—	—	—
Lagena gracillima	—	—	—	—	—	—	—	—	—	—	—	—	3
Lagena cf. *gracillima*	—	—	—	—	—	1	—	—	—	—	—	—	—
Lagena cf. *implicata*	—	—	—	—	—	1	—	—	1	—	—	—	—
Lagena semilineata	—	—	—	—	—	1	—	—	—	—	—	—	—
Lagena cf. *semistriata*	—	—	—	—	—	1	—	—	—	—	—	—	—
Lagena subacuticosta	—	—	1	—	—	—	—	—	—	—	—	—	2
Lagena sulcata	—	—	1	—	—	—	—	—	—	—	—	—	2
Planularia patens	—	—	1	—	—	—	—	—	—	—	—	—	—
Oolina lineata	—	—	—	—	—	2	—	—	—	—	—	—	—
Oolina striatopunctata gemma	—	—	—	—	—	4	—	—	—	—	—	—	—
Oolina sp. I	—	—	—	—	—	1	—	—	—	—	—	—	—
Oolina sp. II	—	—	1	—	—	—	—	—	—	—	—	—	—
Bolivina compacta	—	1	—	—	—	—	—	—	—	—	—	—	—
Bolivina doniezi	—	—	—	—	—	1	—	—	—	—	—	—	—
Bolivina perforatum	—	—	—	—	—	10	—	—	—	—	—	—	—
Bolivina pseudoplicata	—	—	—	—	—	3	—	—	3	—	—	—	—
Bolivina robusta	—	—	—	—	—	3	—	—	2	—	—	—	—
Bolivina sp.	—	—	3	—	—	—	—	—	—	—	—	—	—
Brizalina alata	—	—	1	—	—	—	—	—	—	1	—	—	2
Brizalina striatula	—	—	2	—	—	—	1	—	—	1	—	—	—
Bulimina elongata subulata	—	—	1	—	—	—	—	—	—	—	—	—	—
Bulimina marginata	—	—	—	—	—	1	—	—	—	—	—	—	—
Reussella spinulosa	—	—	—	—	—	2	—	—	—	—	—	—	2
Buliminoides gracilis	—	—	—	—	—	5	1	—	2	1	—	—	10
Buliminoides williamsonianus	—	—	—	—	—	3	—	—	—	—	—	—	13

TABLE 3 (continued)

	Entrance channel								Windang Island				
	59	273	282	297	Y18	Y19	Y20	Y39	Y41	Y42	Y44	Y46	Y52
Uvigerina bassensis	—	—	2	—	3	—	—	—	3	2	—	—	5
Uvigerina cf. *peregrina*	—	—	—	—	—	2	—	—	—	—	—	—	—
Angulodiscorbis quadrangularis	—	—	—	—	—	—	—	—	3	3	—	—	12
Glabratella australensis	—	—	—	—	1	10	—	—	25	10	3	22	86
Glabratella cf. *parri*	—	—	—	—	—	2	—	—	—	—	—	—	—
Glabratella patelliformis	—	—	—	—	—	—	—	—	15	10	—	—	—
Glabratella pulvinata	—	—	—	—	—	—	—	—	2	—	—	—	15
Glabratella tabernacularis	—	—	—	—	—	—	—	—	20	18	—	—	6
Glabratella sp. I	—	—	—	—	—	—	—	—	—	—	—	—	3
Glabratella sp. II	—	—	—	—	—	3	—	—	—	—	—	—	—
Baggina phillippinensis	—	—	—	—	1	—	—	—	6	—	2	—	12
Buccella pustulosa	—	—	—	—	—	—	—	—	—	—	—	—	13
Discorbinella bertheloti	—	—	—	—	—	5	—	—	4	—	—	—	—
Discorbinella planoconcava	—	—	—	—	—	—	—	—	—	1	—	—	—
Lamellodiscorbis dimidiatus	6	—	59	30	14	—	35	3	280	100	40	10	100
Patellinella inconspicua	—	—	—	—	—	—	—	—	16	4	—	—	8
Planulinoides biconcavus	—	—	2	—	—	—	—	—	1	—	—	—	—
Rosalina anglica	—	—	—	—	2	15	—	—	230	220	—	10	180
Rosalina australis	—	—	1	—	10	10	8	—	170	50	—	—	90
Rosalina bradyi	—	—	—	—	—	50	—	—	230	80	3	9	60
Lamarckina sp.	—	—	—	—	—	2	—	—	—	—	—	—	—
Cymbaloporetta bradyi	—	—	—	—	—	3	—	—	10	2	20	—	78
Acervulina inhaerens	—	—	—	—	2	5	3	—	5	10	—	—	29
Planorbulina mediterranensis	—	—	—	—	2	5	3	—	5	10	—	—	29
Cribrononion sydneyensis	—	37	—	—	—	—	—	—	—	—	—	—	—
Elphidium advenum	—	—	4	—	1	—	—	—	—	10	—	—	—
Elphidium argenteus	—	—	—	—	—	—	—	—	—	—	—	—	39
Elphidium crispum	—	1	5	—	50	70	20	3	100	10	—	—	130
Elphidium depressulum	—	—	—	—	—	10	—	—	20	—	—	22	31
Elphidium jenseni	—	—	2	—	2	12	6	—	60	20	10	—	—
Elphidium macellum	—	1	—	—	5	20	10	—	130	20	—	18	180
Elphidium sp.	—	—	—	—	—	3	—	1	—	—	—	—	—
Parrellina imperatrix	—	—	2	4	—	—	4	1	—	3	—	—	24
Nonion depressulus	—	—	—	—	—	3	—	—	—	—	—	—	—

TABLE 3 (concluded)

	Entrance channel								Windang Island				
	59	273	282	297	Y18	Y19	Y20	Y39	Y41	Y42	Y44	Y46	Y52
Nonionella auris	—	1	—	—	—	10	—	—	10	10	—	—	25
Ammonia beccarii	—	70	—	—	50	80	35	2	20	10	5	—	20
Rotalia perlucida	—	—	—	—	—	—	—	—	—	—	—	—	8
Cibicides cygnorum	—	—	13	4	10	—	10	2	40	30	5	—	86
Cibicides refulgens	—	—	—	—	—	—	—	—	—	—	—	—	30
Dyocibicides biserialis	—	—	—	—	5	—	4	—	10	10	—	—	60
Anomalina nonionoides	—	—	13	1	2	5	—	—	—	—	—	—	—
Patellina corrugata	—	—	—	—	—	—	—	—	—	—	—	—	18
Spirillina denticulata	—	—	—	—	—	2	—	—	—	—	—	—	—
Spirillina inaequalis	—	—	—	—	—	—	—	—	—	4	—	—	—
Spirillina tuberculata	—	—	—	—	—	1	—	—	—	—	—	—	—
Spirillina vivipara	—	—	10	—	—	—	—	—	—	—	—	—	34
Spirillina sp.	—	—	—	—	—	1	—	—	—	—	—	—	—
Globigerina bulloides	—	—	1	—	2	3	2	—	10	—	—	—	—
Globigerina sp.	—	—	—	—	—	—	—	—	—	—	—	—	10
Globigerinoides ruber	—	—	—	—	—	5	3	—	10	—	4	—	10
Globoquadrina dutertrei	—	—	—	—	—	2	5	—	—	—	—	—	—
Orbulina universa	—	—	—	—	—	1	2	—	—	—	—	—	—
Pulleniatina obliqueloculata	—	—	—	—	2	—	—	—	—	—	—	—	—
Globorotalia hirsuta	—	—	—	—	—	1	—	—	3	—	—	—	—
Globorotalia (Turborotalia) inflata	—	2	2	—	3	—	2	2	4	—	1	—	4

Fig. 2. Total number of benthonic foraminifers in 100cc of sediment at each sample site.

moderate sea grass coverage in the northern and southern parts of the lagoon respectively (thus accounting for their poor correlation with the more uniformly distributed textulariinid species in the sandy lagoon margin sediments — Fig. 7).

The entrance channel and Windang Island samples contain a mixed assemblage of intertidal and subtidal benthonic foraminifers and a few planktonic species (Table 3; Fig. 8). This is a typical intertidal population which is similar to many other areas on the N.S.W. coast (e.g., Albani, 1968, 1979; Albani and Johnson, 1976).

Foraminifers from a constant volume of each sample from the area studied were subjected to R-mode and Q-mode multivariate analysis. Based on similarity levels and grouping of samples (Figs 7-8) the following four distinct assemblages (Fig. 9) were recognized within the studied area.

Fig. 3. Distribution of rotaliinids in Lake Illawarra (in percent).

Assemblage I

This assemblage (27 samples) occurs in the deepest parts of the lake on a silty clay substrate. It is dominated by *Ammonia beccarii* (52.7%) and *Cribrononion sydneyensis* (43.9%) with subordinate *Triloculina oblonga* (3.0%). Another six species of textulariinids and miliolinids comprise less than 0.4% of the total fauna in this assemblage and mainly occur in samples from close to the lake margin.

Assemblage II

The 37 samples comprising Assemblage II have even more limited foraminiferal diversity. It is dominated by *Ammonia beccarii* (83.2%) and *Cribrononion sydneyensis* (16.4%). Only two other species occur in this assemblage, namely *Ammobaculites foliaceus* (0.4%) and *Miliolinella subrotunda* (0.03%).

Fig. 4. Distribution of *Cribrononion sydneyensis* in Lake Illawarra (in percent).

Assemblage III

Assemblage III occurs in the four areas around the margins of the lake where nutrient supplies are greatest (that is, adjacent to the tidal entrance channel), Macquarie Rivulet and Mullet Creek deltas and Griffins Bay. In all these areas the substrate is predominantly sand and the flora is dominated by *Zostera capricorni* Aschers. The 15 samples are dominated by textulariinids (10 species, 49.6%), rotalids (6 species, 44.8%) and *Miliolinella subrotunda* (5.6%). The main textulariinid species are *Ammobaculites foliaceus* (18.2%), *Tritaxis conica* (10.5%), *Trochammina inflata* (7.6%) and *Eggerella australis* (6.3%) and the two dominant rotaliinids are the lagoonal *Ammonia beccarii* (33.3%) and *Cribrononion sydneyensis* (10.5%).

Assemblage IV

The fourth assemblage consists of a mixture of predominantly marine foraminifers (Fig. 8), some of which represent a life assemblage. Approximately half of the species

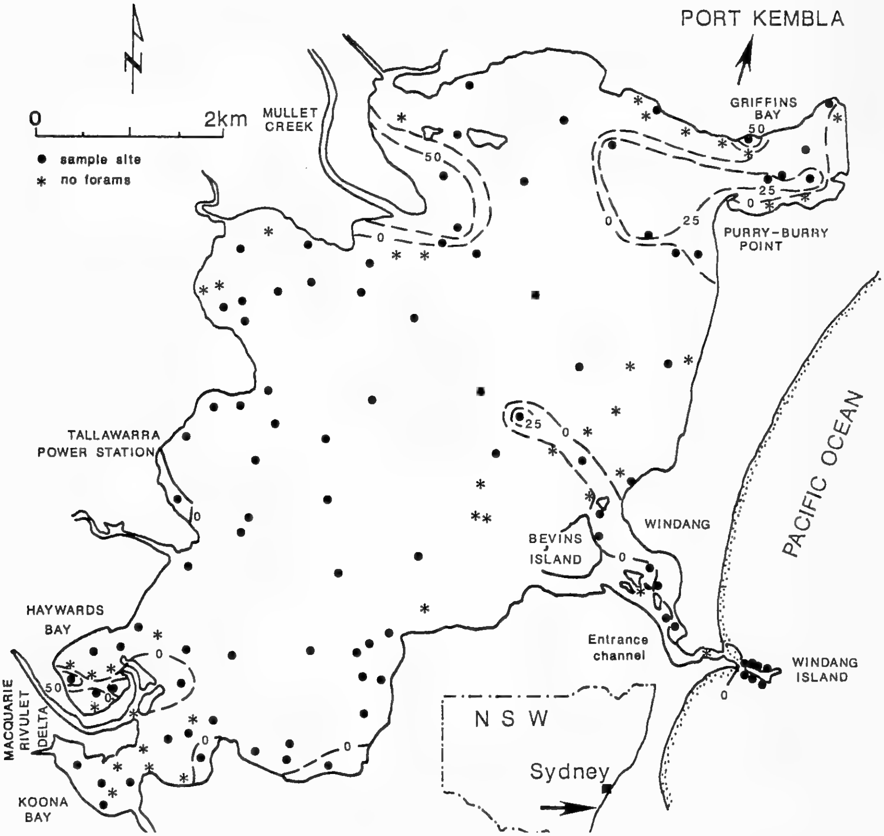


Fig. 5. Distribution of textulariinids in Lake Illawarra (in percent).

probably have been reworked from subtidal environments into Assemblage IV and are only represented by a few specimens. The tidal entrance channel and Windang Island areas have 55 species in common and of these 35 species probably represent live species based on more than 8 specimens being present at a sample site.

The most abundant species constituting an average of 70% of the population at each site in Assemblage IV are:

	Mean number of individuals	Mean % abundance at each location
Lamellodiscorbis dimidiatus	56.5	27.1
Rosalina anglica	54.8	5.0
Elphidium crispum	40.7	9.0
Rosalina bradyi	36.0	3.9
Elphidium macellum	31.9	3.6
Rosalina australis	27.6	2.8
Quinqueloculina subpolygona	23.7	4.6
Ammonia beccarii	18.8	7.1
Cibicides cygnorum	16.7	4.6
Glabratella australensis	13.1	2.2

Fig. 6. Distribution of miliolinids in Lake Illawarra (in percent).

The mixed nature of this tidal assemblage is clearly illustrated in Fig. 8 and consists of lagoonal, intertidal and subtidal species forming a complex thanatocoenose. Minor subdivisions of this assemblage are dependent upon preferential association with particular algal species, especially coralline algae and *Zonaria.*

LAKE ILLAWARRA FORAMINIFERAL COMMUNITIES

The assemblages in Lake Illawarra and its tidal entrance channel are very typical of estuarine lagoons with restricted tidal circulation (e.g., Apthorpe, 1980; Cotter, 1980; Michie, 1982; and Murray, 1973). The distribution pattern and species diversity of foraminifers in the Lake Illawarra area can be used as a basis for distinguishing mud- and sand-dominated lagoonal environments from tidal channel and more open estuarine bay environments such as Broken Bay (Albani, 1978) and Botany Bay (Albani, 1981).

The foraminiferal assemblages in Lake Illawarra can be directly related to the floral communities with the greatest diversity of foraminifers occurring in the seagrass beds

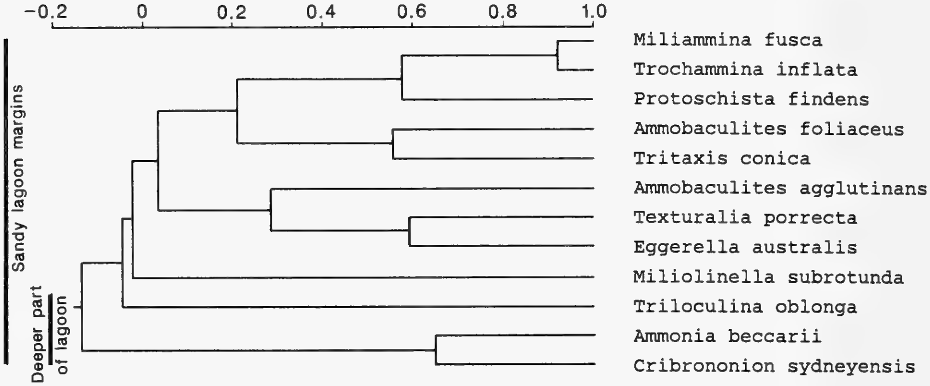


Fig. 7. R-mode cluster dendrogram for species occurring at more than two localities within Lake Illawarra. *Ammonia beccarii* and *Cribrononion sydneyensis* form a distinct group characteristic of deeper water or silty sediments whereas the textulariinids characterize shallow sandy substrates.

where there is relatively low turbidity, a low mud content and an abundant oxygen supply. However, these areas are subject to wider fluctuations in pH and Eh, as well as moderate variations in salinity and temperature, compared with the main body of the lagoon where circulation is less restricted. Foraminiferal faunas on the lagoon margins are dominated by typical euryhaline eurythermal lagoonal species such as *Cribrononion sydneyensis*, *Ammonia beccarii*, *Miliolinella subrotunda* and textulariinids (Fig. 7; Table 2). In the higher energy, wave-influenced margins of the shallow lagoon sandflats the substrate is too mobile for colonization by and preservation of foraminifers and most samples in these regions were barren.

In the deeper portion of Lake Illawarra and in sheltered shallower regions mud is the dominant substrate and, together with the relatively high turbidity, prevents the establishment of seagrass beds. In these areas the foraminiferal diversity is very low (only one or two dominant rotaliinid species) but the population densities range up to 350 specimens per 100cc of sample, the highest density in the lagoon system (Fig. 2). A few shallow water areas within the muddy facies have large accumulations of decaying organic matter (e.g., parts of Griffins, Haywards and Koona bays) resulting in anaerobic bottom conditions which inhibit benthonic foraminifers colonizing these areas. This assemblage therefore shows a great range in foraminiferal abundance which is dependent on a number of environmental factors, not just salinity variation.

The tidal entrance channel to the lagoon is characterized by a very diverse total foraminiferal population with a mixed assemblage of both marine and lagoonal species. Few foraminiferal species live in the mobile sandy tidal channel, which contains a partially abraded mixed marine and estuarine fauna, whereas the seagrass banks along the channel margins support a diverse assemblage with strong shallow marine affinities. The only major distinction between this facies and intertidal open marine facies is the greater abundance of reworked lagoonal species in the tidal channel (although they form less than 2% of the foraminifera population in the channel area).

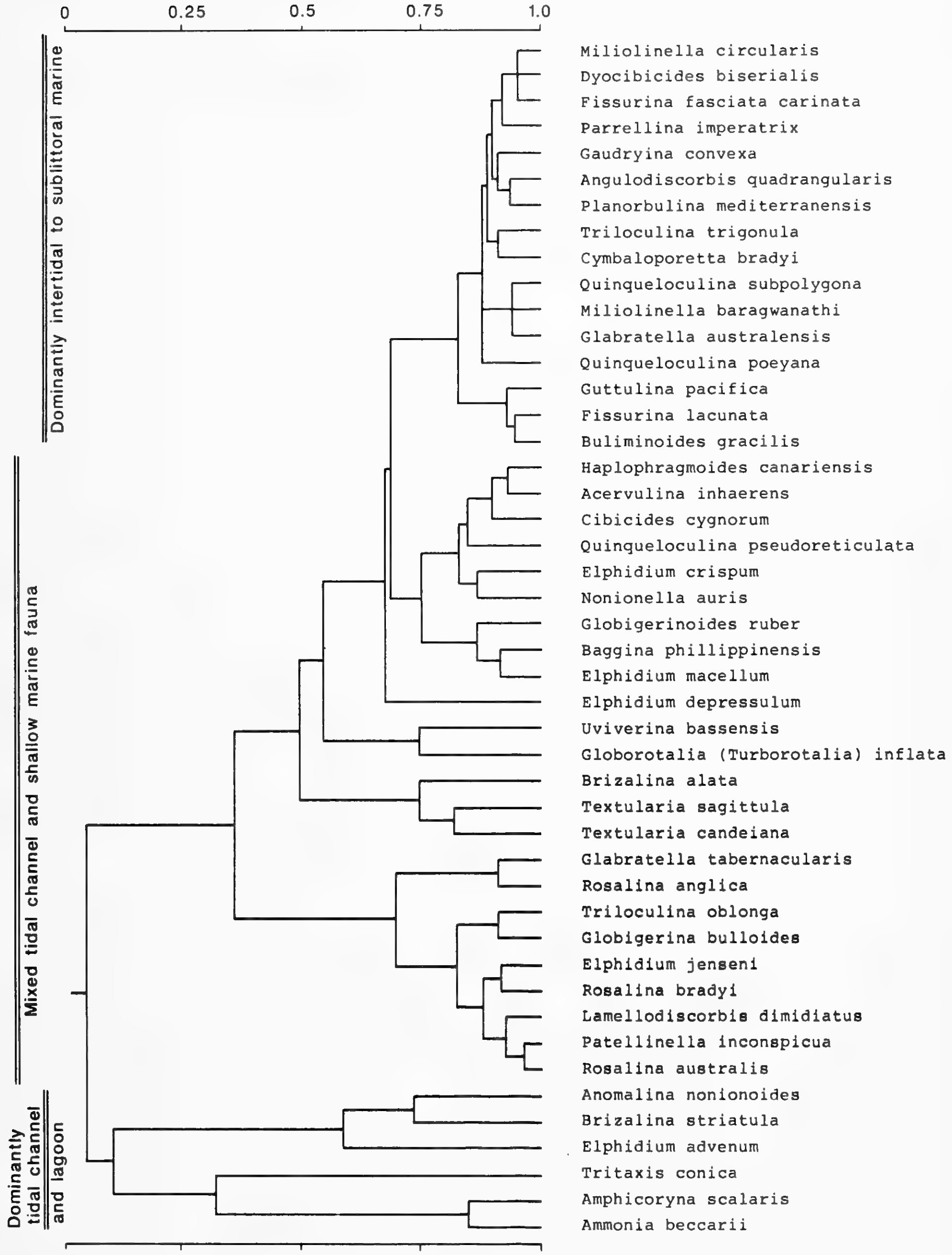


Fig. 8. R-mode cluster dendrogram for species occurring at more than two localities in the tidal channel and around Windang Island. A closely correlated, dominantly marine fauna shows strong similarity to the mixed assemblage of the tidal channel whereas these assemblages show very poor correlation with the lagoonal to tidal channel group.

Fig. 9. Foraminiferal assemblages in Lake Illawarra defined by Q-mode cluster analysis.

ESTUARINE FORAMINIFERAL COMMUNITIES IN N.S.W.

Distribution patterns and species diversity of foraminiferal faunas in the estuarine environments along the coast of New South Wales show two distinct ecological situations. The first is a low diversity and low to moderate population density model, typified by examples of shallow coastal lagoons such as Lake Illawarra, Narrabeen Lagoon, Tuggerah Lake and Lake Macquarie. The second type exhibits high-diversity and medium-density populations in drowned valleys and estuaries, illustrated by example of Broken Bay, Botany Bay and Jervis Bay. In both models the mixing rate of fresh and saline water masses, and salinity fluctuations, play a determinant role in the faunal distribution. The dynamic setting of the environment and the mobility of the substrate are the main factors controlling faunal distributions within the different salinity zones.

Sand-barrier Coastal Lagoon Foraminiferal Community

In N.S.W. lagoons such as Lake Illawarra, Narrabeen Lagoon and Tuggerah Lake the fine-grained sediment in the main body of the lagoon supports a dominant assemblage of *Ammonia beccarii* and *Cribrononion sydneyensis* together with a few arenaceous species such as *Eggerella australis*, *Textularia porrecta* and *Ammobaculites agglutinans*. Similar assemblages were also observed in Lake Victoria and the Gippsland lake system (Apthorpe, 1980), and in Hardy Inlet, Western Australia (Quilty, 1976). The seagrass beds in the peripheral zone around the margin of these lagoonal environments supports a fauna dominated by arenaceous forms such as *Trochammina inflata*, *Ammobaculites agglutinans* and *Eggerella australis* and a few species of Miliolidae (e.g., *Miliolinella subrotunda* and *Triloculina oblonga*).

The tidal channels connecting these lagoons to the open ocean contain a mixture of reworked forms from the nearby oceanic intertidal zone and the lagoon proper. In Lake Illawarra, 82 species were encountered in the seagrass beds along the banks of the inlet channel where the energy level is more reduced. In the middle of the channel the mobile sandy substrate contains only a minor abraded and reworked microfauna. Hardy Inlet contained 42 species in the connection channel (Quilty, 1976). In Narrabeen Lagoon 38 species were identified in the inlet channel while the main body of the lagoon contains only 12 species (Yassini, in prep.).

Tidal Estuary Foraminiferal Community

In the second estuarine ecological type, where tidal exchange of the watermass is rapid, the diversity and density of the foraminiferal population gradually decreases from the mouth of the bay towards the higher reaches of the estuary.

In Broken Bay, Albani (1978) recorded 181 species of benthonic foraminifers along 40km of estuary. The density of the foraminifer population was low both at the upstream end of the estuary and at the outer entrance of the estuary. Upstream in the non-tidal section of the estuary, where the fresh and saline water masses meet and oligohaline conditions prevail, only a few arenaceous foraminifers were found. In the main section of the estuary where there is little change in salinity, the fauna is mostly dominated by Miliolidae (31 species) and Nodosariidae (23 species). Where the estuary has a restricted oceanic connection, foraminifer populations decrease in diversity due to the mobility of the sandy substrate during each tidal cycle.

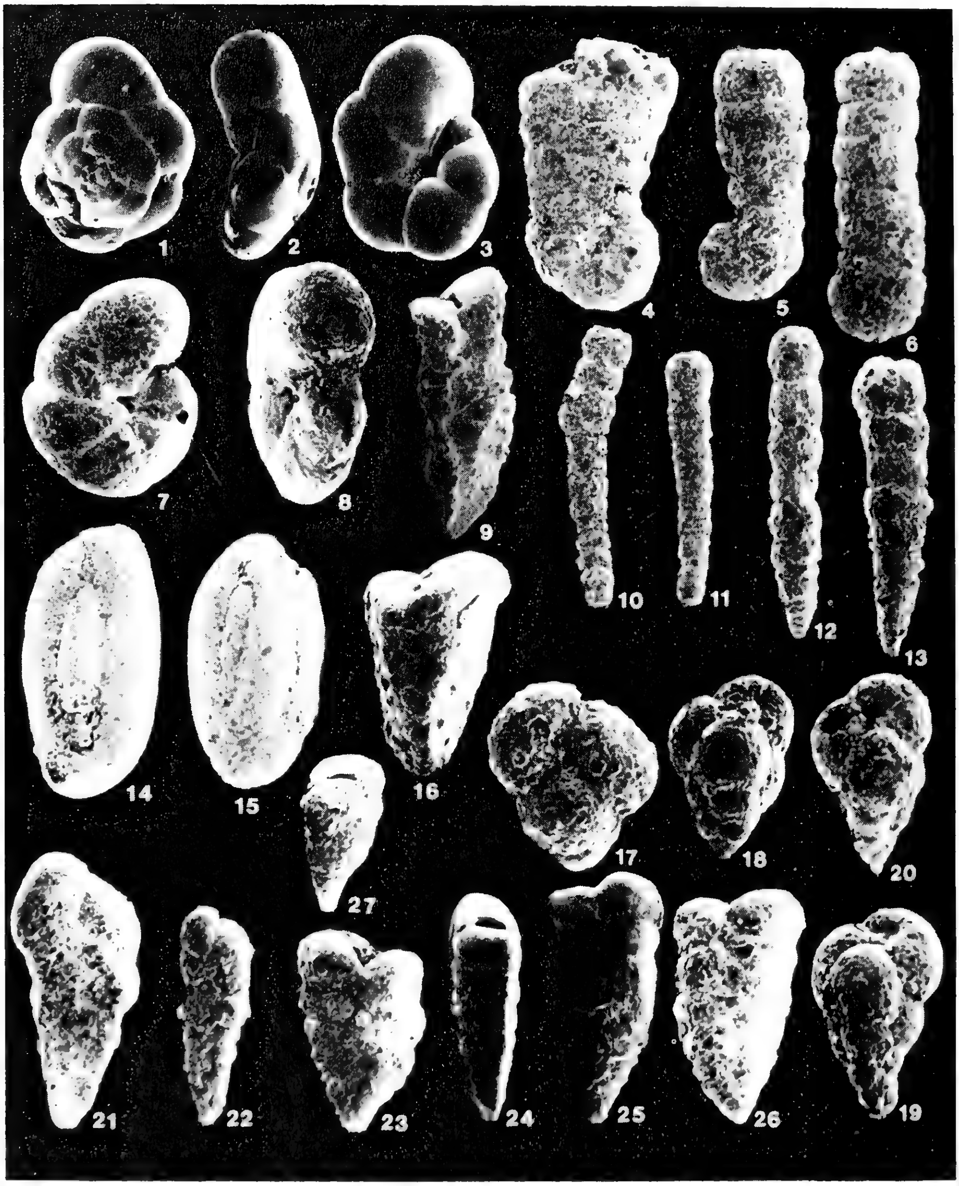
In the Port Hacking estuary, Albani (1968) recorded 119 species of foraminifers along a 10.4km stretch of the estuary. In the weakly-tidal fluvial-dominated section of the estuary only 15 species were found. A maximum diversity of 108 species was found in the main tide-dominated section of the estuary where Miliolidae were represented by 18 species (only 15% of the total fauna). Based on both foraminifer and ostracod distributions, the ecological model in Port Hacking is intermediate between a typical open oceanic bay and a lagoon (Yassini and Wright, 1988).

Open Ocean Foraminiferal Communities

In the upper intertidal zone along the foreshore of Windang Island near the oceanic end of the entrance channel to Lake Illawarra, the foraminiferal density and diversity are typical of an open ocean embayment environment. In the zone 85 species were recorded with Nodosariidae (8 species) and Miliolidae (16 species) forming a prominent component of the foraminiferal assemblage. Foraminiferal assemblages in the open ocean are controlled by the substrate, energy and depth of the environment but a discussion of these facies is beyond the scope of this paper.

ACKNOWLEDGEMENTS

The authors wish to acknowledge their indebtedness to Mrs Anne Clarke, Secretary of the Lake Illawarra Management Committee, and to the Management Committee for their support and encouragement. Dr A. J. Wright reviewed the manuscript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and provided many useful suggestions. Dr A. D. Albani checked some of the species identifications. Most of the SEM micrography was kindly undertaken by the electron microscope unit at the University of Sydney. The use of facilities and technical assistance from the Department of Geology, University of Wollongong, are gratefully acknowledged.

Grants from the Illawarra Region of Councils (1984-1985 Regional Community Development Programme) and from the University of Wollongong enabled this study to be undertaken.

References

ALBANI, A. D., 1968. — Recent Foraminiferida from Port Hacking, New South Wales. *Contr. Cushman Fdn foramin. Res.* 19: 85-119.

——, 1974. — New benthonic Foraminiferida from Australian waters. *J. foramin. Res.* 4: 33-39.

——, 1978. — Recent Foraminifera of an estuarine environment in Broken Bay, New South Wales. *Aust. J. mar. Freshwat. Res.* 29: 355-398.

——, 1979. — Recent shallow water Foraminifera from New South Wales. *Australian Marine Science Association Handbook* 3: 1-57.

——, 1981. — Pleistocene Foraminifera from Botany Bay, New South Wales. *Alcheringa* 5: 147-160.

——, and JOHNSON, K. R., 1976. — Resolution of foraminiferal biotopes in Broken Bay, New South Wales. *J. geol. Soc. Aust.* 21: 435-446.

ANDERSON, J. R., and STORY, K. J., 1981. — Temperature, salinity, turbidity and tidal data for eight estuaries on the south coast of New South Wales, 1974-1978. *Tech. Memo. Commonw. scient. ind. Res. Org.* 81/20.

——, ——, and CAROLANE, R., 1981. — Macrobenthic fauna and sediment data for eight estuaries on the south coast of New South Wales. *Tech. Memo. Commonw. scient. ind. Res. Org.* 81/22.

APTHORPE, M., 1980. — Foraminiferal distribution in the estuarine Gippsland Lakes system, Victoria. *Proc. Roy. Soc. Vict.* 91: 207-232.

BARKER, R. W., 1960. — Taxonomic notes on the species figured by H. B. Brady in his report on the Foraminifera dredged by H.M.S. Challenger during the years 1873-1876. *Spec. Publs Soc. econ. Paleont. Miner.*, Tulsa 9: 1-238.

BRADY, H. B., 1884. — Report on the Foraminifera dredged by H.M.S. Challenger during the years 1873-1876. *Challenger Expedition Report, Zoology* 9: 1-814.

CANN, J. H., and GOSTIN, V. A., 1985. — Coastal sedimentary facies and foraminiferal biofacies of the St. Kilda Formation at Port Gawler, South Australia. *Trans Roy. Soc. S. Aust.* 109: 121-142.

CARTER, A. N., 1964. — Tertiary Foraminifera from Gippsland, Victoria, and their stratigraphical significance. *Mem. geol. Surv. Vict.* 23: 1-154.

CLARKE, D. J., and ELIOT, I. G., 1984. — Wind driven water circulation in Lake Illawarra, New South Wales: a numerical simulation. *University of Wollongong Coastal Research Report* 2/84.

CHAPMAN, F., and PARR, W. J., 1937. — Foraminifera. *Australian Antarctic Expedition 1911-1914 Scientific Report* Series G.

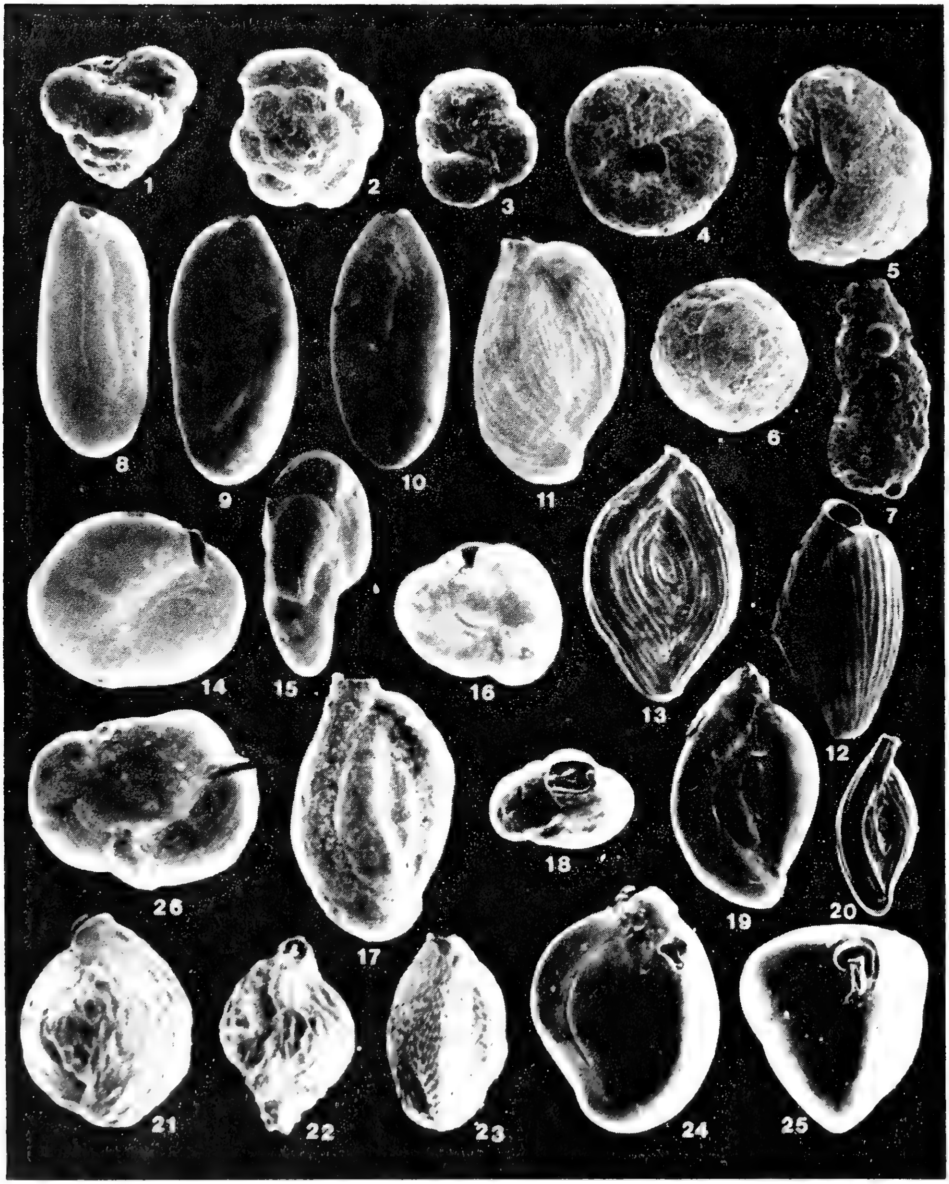
COLLINS, A. C., 1958. — Foraminifera. *Great Barrier Reef Expedition 1928-1929 Report* 6: 335-436.

——, 1974. — Port Phillip survey 1957-1963, Foraminiferida. *Mem. Nat. Mus. Vict.* 35: 1-62.

COTTER, L. K., 1980. — The distribution of Foraminiferida in the Clyde River estuary, Batemans Bay, N.S.W. North Ryde, N.S.W.: Macquarie University, B.A. (Hons) thesis, unpubl.

CUSHMAN, J. A., 1932. — The Foraminifera of the tropical Pacific collections of the Albatross, 1899-1900. *Bull. U.S. natn. Mus.* 161, Pt 1.

Fig. 10. **1-3,** *Trochammina inflata* Sample 245, Lake Illawarra. x54 Spiral, apertural and umbilical views; **4,** *Ammobaculites foliaceus* Sample Y15, Lake Illawarra. x50 Spiral view; **5,** *Ammobaculites agglutinans* Sample Y13, Lake Illawarra. x 55 Spiral view; **6,** *Ammobaculites* sp. Sample Y10, Lake Illawarra. x50 Spiral view; **7-8,** *Haplophragmoides canariensis* Sample Y52, Windang Island. x47. Umbilical and apertural views; **9, 16,** *Gaudryina convexa* Sample Y52, Windang Island. x25, x44 Lateral views; **10-11,** *Protoschista findens* Sample 306, Lake Illawarra. x50 Lateral views; **12-13,** *Reophax* sp. Sample Y13, Lake Illawarra. x75 Lateral views; **14-15,** *Miliammina fusca* Sample 245, Lake Illawarra. x71 Lateral views; **17-20,** *Eggerella australis* Sample 138, Lake Illawarra. x80 Lateral and apertural views; **21,** *Textularia* sp. I Sample Y52, Windang Island. x78 Lateral view; **22,** *Textularia porrecta* Sample Y30, Lake Illawarra. x50 Lateral view; **23, 27,** *Textularia candeiana* Sample Y42, Windang Island. x57, x60 Lateral and apertural views; **24, 25,** *Textularia sagittula* Sample Y52, Windang Island. x38 Apertural and lateral views; **26,** *Textularia* sp. II Sample Y52, Windang Island. x48 Lateral view.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——, 1933. — The Foraminifera of the tropical Pacific collections of the Albatross, 1899-1900. *Bull. U.S. natn. Mus.* 161, Pt 2.

——, 1942. — The Foraminifera of the tropical Pacific collections of the Albatross, 1899-1900. *Bull. U.S. natn. Mus.* 161, Pt 4.

ELIOT, I. G., YOUNG, R. W., and CLARKE, D. J., 1976. — Lake hydrology. *An Environmental Assessment Project, City of Wollongong Council and University of Wollongong*, 41-50.

ELLIS, J., and KANAMORI, S., 1977. — Water pollution studies on Lake Illawarra. III Distribution of heavy metals in sediments. *Aust. J. mar. Freshwat. Res.* 28: 485-96.

——, ——, and LAIRD, P. G., 1977. — Water pollution studies on Lake Illawarra. I Salinity variation and estimation of residence time. *Aust. J. mar. Freshwat. Res.* 30: 467-77.

GIBBS, P. J., 1986. — Five N.S.W. barrier lagoons; their macrobenthic fauna and seagrass communities. Kensington, N.S.W.: University of New South Wales, Ph.D. thesis, unpubl.

HARRIS, M., 1976a. — Ecological milieu of Lake Illawarra. *An Environmental Assessment Project, City of Wollongong Council and University of Wollongong*, 51-65.

——, 1976b. — The biota of Illawarra Lake. *An Environmental Assessment Project, City of Wollongong Council and University of Wollongong*, 66-76.

HARRIS, J., 1977. — Ecological studies on Illawarra Lake with special reference to *Zostera capricorni* Ascherson. Kensington, N.S.W.: University of New South Wales, M.Sc. thesis, unpubl.

HEAN, D., and NANSON, G., 1985. — Geomorphological investigation of stream channels and alluvial deposits in areas of proposed urban development within the catchment of Lake Illawarra. *Report for New South Wales State Pollution Control Commission, Uniadvice, University of Wollongong.*

HERMELIN, J. O. R., and SCOTT, D. B., 1985. — Recent benthonic Foraminifera from the north central Atlantic. *Micropaleontology* 31: 199-220.

JONES, B. G., ELIOT, I. G., and DEPERS, A. M., 1976. — Sediments in Lake Illawarra. *An Environmental Assessment Project, City of Wollongong Council and University of Wollongong*, 20-40.

KOHL, B., 1985. — Early Pliocene benthonic foraminifers from the Salina Basin, southeastern Mexico. *Bull. Am. Paleont.* 88: 1-173.

LOEBLICH, A. R., and TAPPAN, H., 1964. — *Treatise on Invertebrate Paleontology.* Part C: *Protista*, Vols 1-2. Lawrence, Kansas: Univ. Kansas Press.

——, and ——, 1974. — Recent advances in the classification of the Foraminiferida. *Foraminifera* 1: 1-53.

——, and ——, 1984. — Suprageneric classification of the Foraminiferida (Protozoa). *Micropaleontology* 30: 1-70.

MATOBA, Y., 1970. — Distribution of Recent shallow-water Foraminifera of Matsushima Bay, Miyagi Prefecture, northwest Japan. *Sci. Rep. Tohoku Univ., Series 2 (Geol.)* 42: 1-85.

MCCULLOCH, I., 1977. — *Quantitative observations on Recent foraminiferal tests with emphasis on the eastern Pacific*, Pts 1-3. University of Southern California Publication.

——, 1981. — *Quantitative observations on Recent foraminiferal tests with emphasis on the eastern Pacific*, Pt 4. University of Southern California Publication.

MICHIE, M. G., 1982. — Use of the Bray-Curtis similarity measure in cluster analysis of foraminiferal data. *J. Math. Geol.* 14: 661-667.

MURRAY, J. W., 1973. — *Distribution and Ecology of Living Benthonic Foraminiferids.* London: Heinemann Educational Books.

——, 1975. — *An Atlas of British Recent Foraminiferids.* London: Heinemann Educational Books.

PARR, W. J., 1932. — Victorian and South Australian shallow water Foraminifera: Part 2. *Proc. Roy. Soc. Vict.* 44: 218-234.

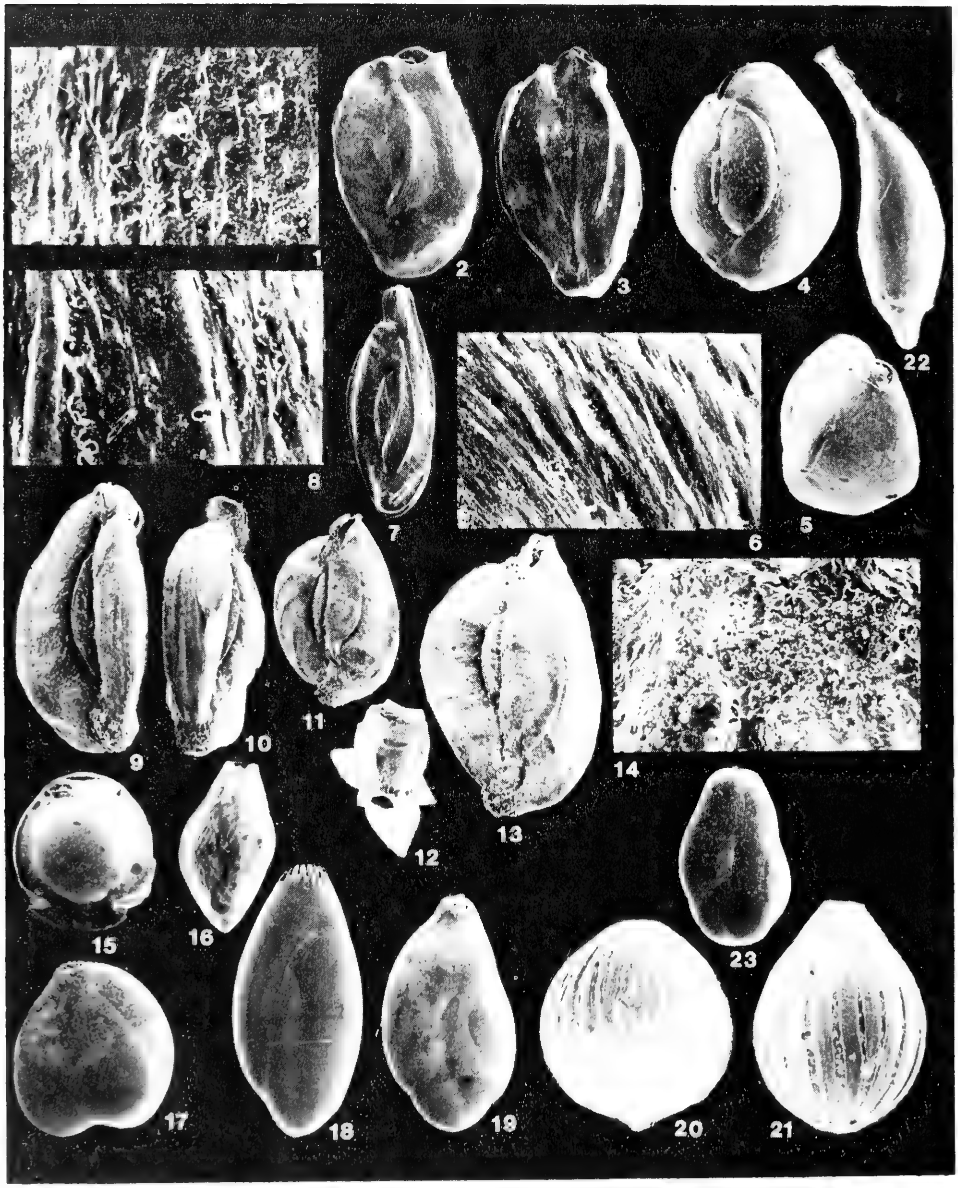
——, 1945. — Recent Foraminifera from Barwon Heads, Victoria. *Proc. Roy. Soc. Vict.* 56: 189-218.

——, 1950. — Foraminifera. *British and New Zealand Antarctic Research Expedition 1929-1931 Report* Series B, 5: 233-392.

POAG, C. W., 1981. — *Ecologic Atlas of Benthic Foraminifera of the Gulf of Mexico.* Hutchinson Ross Publ., 174 pp.

PUBLIC WORKS DEPARTMENT, N.S.W., 1985. — *Lake Illawarra Entrance Study*, 109 pp.

Fig. 11. **1-3,** *Eggerella subconica* Sample Y41, Windang Island. x53 Umbilical, spiral and apertural views; **4-6,** *Tritaxis conica* Sample 282, tidal channel. x100 Apertural, lateral and spiral views; **7,** *Ammotium cassis* Sample Y30, Lake Illawarra. x56 Lateral view; **8-10,** *Triloculina oblonga* Sample Y33, Lake Illawarra. x70 Spiral and lateral views; **11-12,** *Quinqueloculina poeyana* Sample Y41, Windang Island. x57 Spiral and apertural views; **13, 20,** *Spiroloculina antillarum* Sample Y52, Windang Island. x31 Spiral views; **14-16,** *Miliolinella circularis* Sample Y42, Windang Island. x70 Spiral and apertural views; **17-18,** *Quinqueloculina tropicalis* Sample Y41, Windang Island. x70 Spiral and apertural views; **19,** *Spiroloculina communis* Sample Y52, Windang Island. x36 Spiral view; **21-22,** *Quinqueloculina* sp. nov. Sample Y52, Windang Island. x47 Spiral and apertural views; **23,** *Quinqueloculina pseudoreticulata* Sample Y19, tidal channel. x18 Apertural view; **24-25,** *Triloculina trigonula* Sample Y52, Windang Island. x61 Spiral and apertural views; **26,** *Miliolinella circularis* subsp. nov. Sample Y52, Windang Island. x43 Spiral view.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QUILTY, P. G., 1976. — Foraminifera of Hardy Inlet, southwestern Australia. *J. Proc. Roy. Soc. West. Aust.* 59: 79-90.

ROY, P. S., and PEAT, C., 1975. — Bathymetry and bottom sediments of Lake Illawarra. *Rec. geol. Surv. N.S.W.* 17: 65-79.

SEIBOLD, I., 1975. — Benthonic Foraminifera from the coast and lagoon of Cochin (South India). *Revista española Micropaleontologia* 7: 175-213.

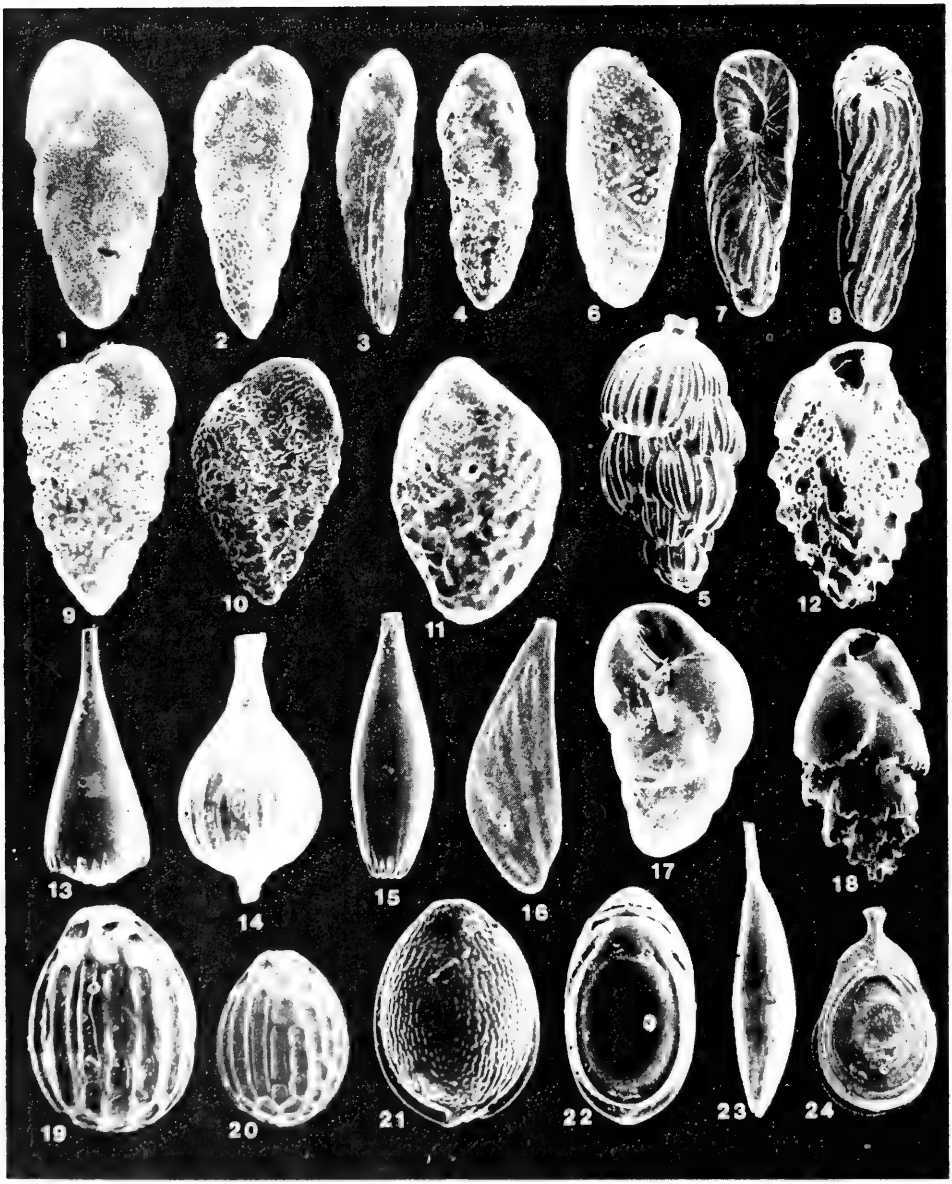
SIDEBOTTOM, H., 1912. — Lagenae of the south-west Pacific Ocean, from soundings taken by H.M.S. Waterwitch 1895. *J. Quekett microsc. Club*, ser. 2 70: 375-437.

——, 1913. — Lagenae of the south-west Pacific Ocean, from soundings taken by H.M.S. Waterwitch 1895. *J. Quekett microsc. Club*, ser. 2, *Supplementary Paper 12*, 73: 161-210.

YASSINI, I., and JONES, B. G., 1987. — Ostracoda in Lake Illawarra: environmental factors, assemblages and systematics. *Aust. J. mar. Freshwat. Res.*, 38: 795-843.

——, and WRIGHT, A. J., 1988. — Distribution and ecology of Recent ostracodes from Port Hacking, New South Wales. *Proc. Linn. Soc. N.S.W.* 10: 159-174.

Fig. 12. **1-3,** *Quinqueloculina subpolygona* Sample Y52, Windang Island. Details of ornamentation (x460), spiral views (x31, x54); **4-6,** *Quinqueloculina seminula* Sample 282, tidal channel. Spiral and apertural views (x38), details of ornamentation (x460); **7-8,** *Quinqueloculina granulocostata* Sample Y41, Windang Island. Spiral view (x43), details of ornamentation (x460); **9-14,** *Miliolinella baragwanathi* Sample Y52, Windang Island. Lateral, spiral and apertural views (x72), details of ornamentation (x460); **15,** *Pyrgo subglobulus* Sample Y19, tidal channel. x40 Apertural view; **16,** *Quinqueloculina pseudoreticulata* Sample Y19, tidal channel. x40 Apertural view; **17,** *Sigmoidella elegantissima* Sample Y19, tidal channel. x32 Spiral view; **18,** *Guttulina pacifica* Sample Y19, tidal channel. x72 Spiral view; **19,** *Guttulina* sp. I Sample Y42, Windang Island. x48 Spiral view; **20,** *Oolina lineata* Sample Y19, tidal channel. x93 Lateral view; **21,** *Lagena acuticosta* Sample Y52, Windang Island. x91 Lateral view; **22,** *Lagena gracillima* Sample Y52, Windang Island. x79 Lateral view; **23,** *Guttulina* sp. II Sample Y19, tidal channel. x20 Lateral view.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APPENDIX

SPECIES IDENTIFIED FROM THE LAKE ILLAWARRA AREA

Characteristic features and surface ornamentation of foraminifers from the Lake Illawarra lagoonal, tidal channel and adjacent intertidal environments are listed and illustrated following the classification of Loeblich and Tappan (1964, 1974, 1984). The species are listed in alphabetical order within genera and families and the scanning electron microscope figures show the characteristic features used for their identification.

Family: Rzehakinidae Cushman, 1933
  Genus: *Miliammina* Heron-Allen & Earland, 1930
    Miliammina fusca (Brady, 1870) CPC 27318 (Fig. 10, nos 14-15)

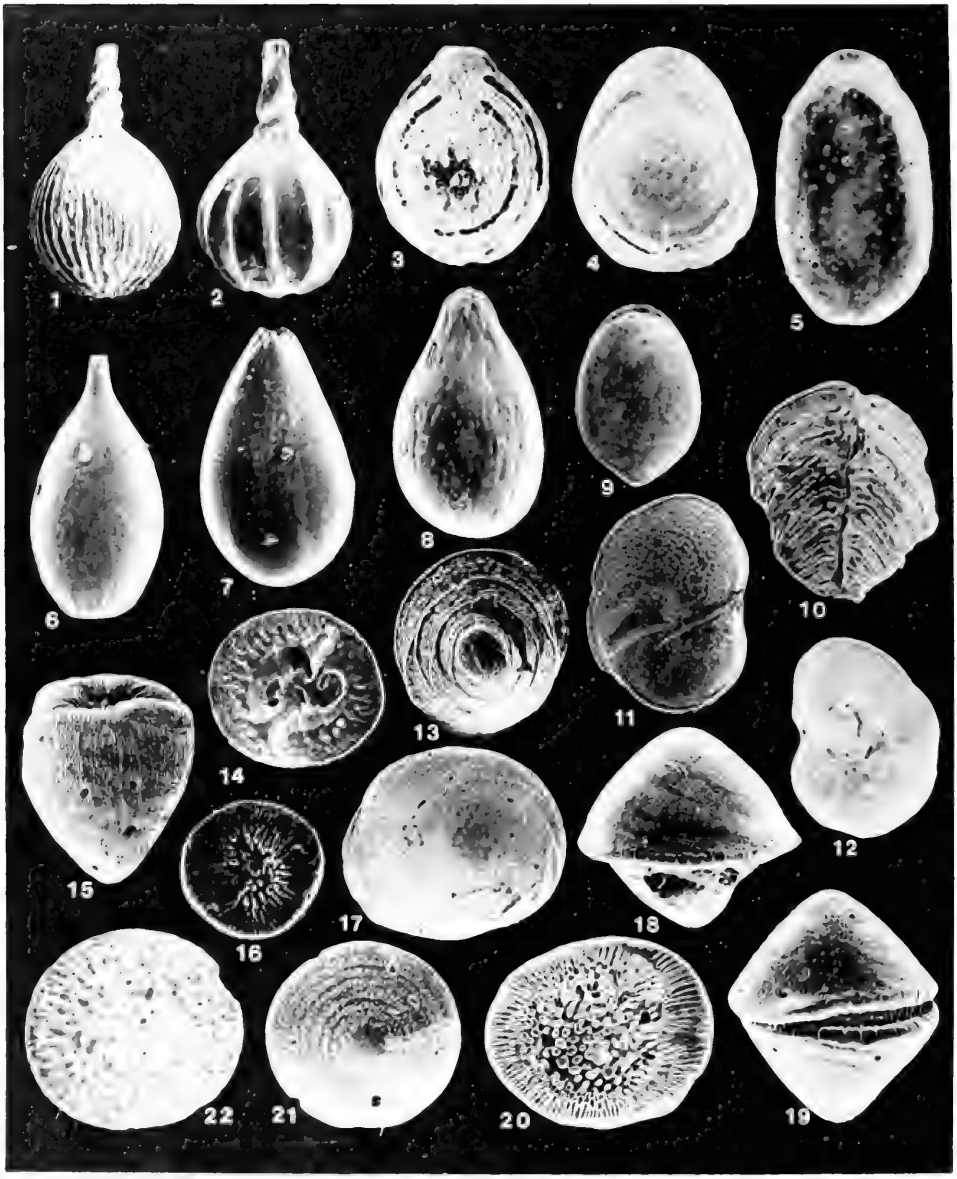
Family: Hormosinidae Haeckel, 1894
  Genus: *Protoschista* Eimer & Fickert, 1899
    Protoschista findens (Parker, 1870) CPC 27319 (Fig. 10, nos 10-11)
  Genus: *Reophax* Montfort, 1808
    Reophax sp. CPC 27320 (Fig. 10, nos 12-13)

Family: Lituolidae de Blainville, 1825
  Genus: *Ammobaculites* Cushman, 1910
    Ammobaculites agglutinans (d'Orbigny, 1846) CPC 27321 (Fig. 10, no. 5)
    Ammobaculites foliaceus (Brady, 1881) CPC 27322 (Fig. 10, no. 4)
    Ammobaculites sp. (Fig. 10, no. 6)
  Genus: *Ammotium* Loeblich & Tappan, 1953
    Amnotium cassis (Parker, 1870) CPC 27323 (Fig. 11, no. 7)
  Genus: *Haplophragmoides* Cushman, 1910
    Haplophragmoides canariensis (d'Orbigny, 1839) CPC 27324 (Fig. 10, nos 7-8)

Family: Trochamminidae Schwager, 1877
  Genus: *Tritaxis* Schubert, 1921
    Tritaxis conica (Parker & Jones, 1865) CPC 27325 (Fig. 11, nos 4-6)
  Genus: *Trochammina* Parker & Jones, 1859
    Trochammina inflata (Montagu, 1808) CPC 27326 (Fig. 10, nos 1-3)

Family: Textulariidae Ehrenberg, 1838
  Genus: *Textularia* Defrance, *in* de Blainville, 1824
    Textularia candeiana (d'Orbigny, 1839) CPC 27327 (Fig. 10, nos 23, 27)
    Textularia porrecta (Brady, 1884) CPC 27328 (Fig. 10, no. 22)
    Textularia sagittula (Defrance, 1824) CPC 27329 (Fig. 10, nos 24-25)
    Textularia sp. I CPC 27330 (Fig. 10, no. 21)
    Textularia sp. II (Fig. 10, no. 26)

Fig. 13. **1,** *Brizalina alata* Sample 282, tidal channel. x65 Lateral view; **2,** *Bolivina doniezi* Sample Y19, tidal channel. x70 Lateral view; **3,** *Brizalina striatula* Sample 282, tidal channel. x71 Lateral view; **4,** *Bolivina robusta* Sample Y19, tidal channel. x117 Lateral view; **5,** *Uvigerina bassensis* Sample 282, tidal channel. x67 Lateral view; **6,** *Bolivina perforatum* Sample Y19, tidal channel. x280 Lateral view; **7,** *Buliminoides gracilis* Sample Y19, tidal channel. x72 Lateral view; **8,** *Buliminoides williamsonianus* Sample Y19, tidal channel. x62 Lateral view; **9-10,** *Bolivina pseudoplicata* Sample Y19, tidal channel. x78, x85 Lateral view; **11,** *Bolivina* sp. Sample 282, tidal channel. x117 Lateral view; **12,** *Reussella spinulosa* Sample Y19, tidal channel. x70 Lateral view; **13,** *Lagena crenata* Sample 282, tidal channel. x86 Lateral view; **14,** *Lagena semilineata* Sample Y19, tidal channel. x122 Lateral view; **15,** *Lagena* cf. *implicata* Sample Y19, tidal channel. x68 Lateral view; **16,** *Planularia patens* Sample 282, tidal channel. x72 Lateral view; **17,** *Bulimina elongata subulata* Sample 282, tidal channel. x126 Lateral view; **18,** *Bulimina marginata* Sample Y19, tidal channel. x84 Lateral-apertural view; **19,20,** *Oolina striatopunctata gemma* Sample Y19, tidal channel. x193, x79 Lateral views; **21,** *Fissurina marginatoperforata* Sample Y19, tidal channel. x118 Lateral view; **22,** *Fissurina sulcata* Sample Y19, tidal channel. x123 Lateral view; **23,** *Lagena* cf. *gracillima* Sample Y19, tidal channel. x78 Lateral view; **24,** *Fissurina* sp. I Sample 282, tidal channel. x100 Lateral view.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Family: Ataxophragmiidae Schwager, 1877
  Genus: *Eggerella* Cushman, 1933
    Eggerella australis (Collins, 1958) CPC 27331 (Fig. 10, nos 17-20)
    Eggerella subconica (Parr, 1950) CPC 27332 (Fig. 11, nos 1-3)
  Genus: *Gaudryina* d'Orbigny, *in* de la Sagra, 1839
    Gaudryina convexa (Karrer, 1865) CPC 27333 (Fig. 10, nos 9, 16)

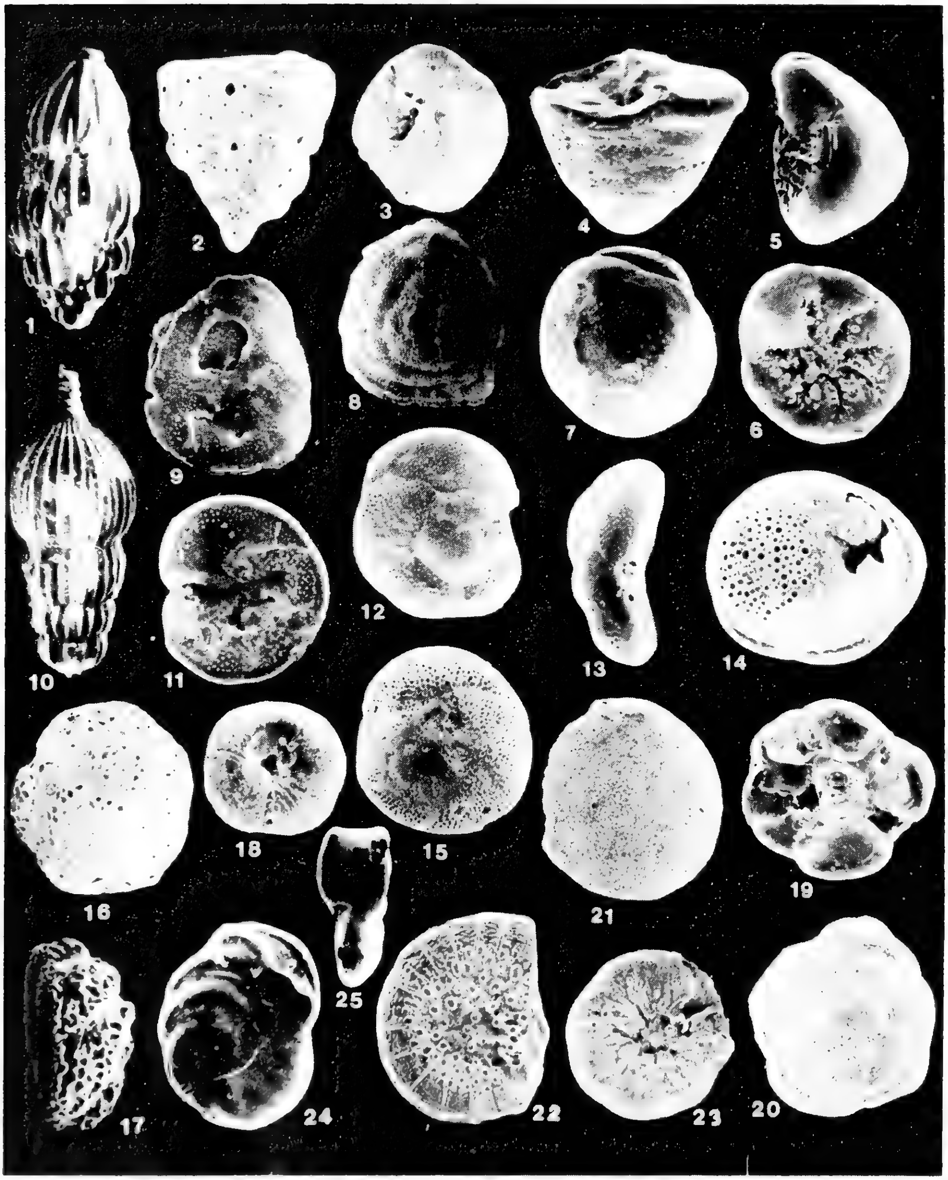
Family: Nubeculariidae Jones, 1875
  Genus: *Spiroloculina* d'Orbigny, 1826
    Spiroloculina antillarum (d'Orbigny, 1839) CPC 27334 & 27335 (Fig. 11, no. 13)
    Spiroloculina communis (Cushman & Todd, 1944) (Fig. 11, no. 19)

Family: Miliolidae Ehrenberg, 1839
  Genus: *Miliolinella* Wiesner, 1931
    Miliolinella baragwanathi (Parr, 1945) CPC 27337 (Fig. 12, nos 9-14)
    Miliolinella circularis (Bornemann, 1855) CPC 27338 (Fig. 11, nos 14-16)
    Miliolinella circularis subsp. nov. CPC 27339 (Fig. 11, no. 26)
    Miliolinella subrotunda (Montagu, 1803) (Fig. 19, nos 1-4)
  Genus: *Pyrgo* Defrance, *in* de Blainville, 1824
    Pyrgo subglobulus (Parr, 1950) CPC 27340 (Fig. 12, no. 15)
  Genus: *Quinqueloculina* d'Orbigny, 1826
    Quinqueloculina granulocostata (Germeraad, 1946) CPC 27341 (Fig. 12, nos 7-8)
    Quinqueloculina poeyana (d'Orbigny, 1839) CPC 27342 (Fig. 11, nos 11-12)
    Quinqueloculina pseudoreticulata (Parr, 1941) CPC 27343 (Fig. 11, no. 23, Fig. 12, no. 16)
    Quinqueloculina seminula (Linné, 1767) CPC 27344 (Fig. 12, nos 4-6)
    Quinqueloculina subpolygona (Parr, 1945) CPC 27345 (Fig. 12, nos 1-3)
    Quinqueloculina tasmanica (Albani, 1978) CPC 27346 (Fig. 11, no. 20)
    Quinqueloculina tropicalis (Cushman, 1924) CPC 27347 (Fig. 11, nos 17-18)
    Quinqueloculina sp. nov. CPC 27348 (Fig. 11, nos 21-22)
  Genus: *Triloculina* d'Orbigny, 1826
    Triloculina oblonga (Montagu, 1803) CPC 27350 & 27351 (Fig. 11, no. 8-10)
    Triloculina tricarinata (d'Orbigny, 1826)
    Triloculina trigonula (Lamarck, 1804) CPC 27352 (Fig. 11, nos 24-25)

Family: Polymorphinidae d'Orbigny, 1839
  Genus: *Guttulina* d'Orbigny, *in* de la Sagra, 1839
    Guttulina pacifica (Cushman & Ozawa, 1928) CPC 27355 (Fig. 12, no. 18)
    Guttulina regina (Brady, Jones & Parker, 1870) CPC 27356 (Fig. 19, no. 5)
    Guttulina sp. I CPC 27357 (Fig. 12, no. 19)
    Guttulina sp. II CPC 27358 (Fig. 12, no. 23)
  Genus: *Sigmoidella* Cushman & Ozawa, 1928
    Sigmoidella elegantissima (Parker & Jones, 1865) CPC 27359 (Fig. 12, no. 17)

Family: Nodosariidae Ehrenberg, 1838
  Genus: *Amphicoryna* Schlumberger, *in* Milne-Edward, 1881
    Amphicoryna scalaris (Batsch, 1791) CPC 27360 (Fig. 15, no. 10)

Fig. 14. **1,** *Lagena subacuticosta* Sample 282, tidal channel. x83 Lateral view; **2,** *Lagena sulcata* Sample 282, tidal channel. x117 Lateral view; **3,** *Fissurina lacunata* Sample Y19, tidal channel. x108 Lateral view; **4,** *Fissurina fasciata carinata* Sample Y52, Windang Island. x102 Lateral view; **5,** *Fissurina* cf. *subquadrata* Sample Y52, Windang Island. x118 Lateral view; **6,** *Lagena* cf. *semistriata* Sample Y19, tidal channel. x67 Lateral view; **7,** *Oolina* sp. I Sample Y19, tidal channel. x117 Lateral view; **8,** *Oolina* sp. II Sample 282, tidal channel. x101 Lateral view; **9,** *Fissurina* sp. II Sample Y19, tidal channel. x83 Lateral view; **10,** *Bolivinella folia* Sample Y19, tidal channel. x77 Lateral view; **11,** *Lamarckina* sp. Sample Y19, tidal channel. x71 Spiral view; **12,** *Lamarckina* sp. Sample Y42, Windang Island. x71 Umbilical view; **13-14,** *Patellina corrugata* Sample Y52, Windang Island. x87 Spiral and umbilical views; **15-16,** *Glabratella tabernacularis* Sample Y42, Windang Island. x91 Spiral and umbilical views; **17-20,** *Glabratella australensis* Sample Y52, Windang Island. x60, x91 Spiral, plastogamic and umbilical views; **21-22,** *Glabratella* sp. I. Sample Y52, Windang Island. x70 Umbilical and spiral views.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Genus: *Bolivinella* Cushman, 1927
    Bolivinella folia (Parker & Jones, 1865) CPC 27361 (Fig. 14, no. 10)
Genus: *Fissurina* Reuss, 1850
    Fissurina fasciata carinata (Sidebottom, 1906) CPC 27362 (Fig. 14, no. 4)
    Fissurina lacunata (Burrows & Holland, 1895) CPC 27363 (Fig. 14, no. 3)
    Fissurina marginatoperforata (Seguenza, 1913) CPC 27364 (Fig. 13, no. 21)
    Fissurina sp. cf. *subquadrata* (Parr, 1945) CPC 27365 (Fig. 14, no. 5)
    Fissurina sulcata (Collins, 1974) CPC 27366 (Fig. 13, no. 22)
    Fissurina sp. I CPC 27367 (Fig. 13, no. 24)
    Fissurina sp. II CPC 27368 (Fig. 14, no. 9)
Genus: *Lagena* Walker & Jacob, *in* Kanmacher, 1798
    Lagena acuticosta (Reuss, 1861) CPC 27369 (Fig. 12, no. 21)
    Lagena crenata (Parker & Jones, 1865) (Fig. 13, no. 13)
    Lagena gracillima (Seguenza, 1862) CPC 27370 (Fig. 12, no. 22)
    Lagena sp. cf. *gracillima* (Seguenza, 1862) CPC 27371 (Fig. 13, no. 23)
    Lagena sp. cf. *implicata* (Cushman & McCulloch, 1950) CPC 27372 (Fig. 13, no. 15)
    Lagena semilineata (Wright, 1866) CPC 27373 (Fig. 13, no. 14)
    Lagena sp. cf. *semistriata* (Williamson, 1848) CPC 27374 (Fig. 14, no. 6)
    Lagena subacuticosta (Parr, 1950) (Fig. 14, no. 1)
    Lagena sulcata (Walker & Jacob, 1798) CPC 27375 (Fig. 14, no. 2)
Genus: *Planularia* Defrance, *in* de Blainville, 1824
    Planularia patens (Brady, 1884) CPC 27376 (Fig. 13, no. 16)

Family: Glandulinidae Reuss, 1860
Genus: *Oolina* d'Orbigny, *in* de la Sagra, 1839
    Oolina lineata (Williamson, 1848) CPC 27377 (Fig. 12, no. 20)
    Oolina striatopunctata gemma (Cushman & McCulloch, 1950) CPC 27378 (Fig. 13, nos 19-20)
    Oolina sp. I CPC 27379 (Fig. 14, no. 7)
    Oolina sp. II CPC 27380 (Fig. 14, no. 8)

Family: Bolivinitidae Cushman, 1927
Genus: *Bolivina* d'Orbigny, *in* de la Sagra, 1839
    Bolivina compacta (Sidebottom, 1905) CPC 27381
    Bolivina doniezi (Cushman & Wickenden, 1928) (Fig. 13, no. 2)
    Bolivina perforatum (Dinapoli, 1946) (Fig. 13, no. 6)
    Bolivina pseudoplicata (Heron-Allen & Earland, 1930) CPC 27382 (Fig. 13, nos 9-10)
    Bolivina robusta (Brady, 1881) CPC 27383 (Fig. 13, no. 4)
    Bolivina sp. CPC 27384 (Fig. 13, no. 11)
Genus: *Brizalina* Costa, 1856
    Brizalina alata (Seguenza, 1862) CPC 27385 (Fig. 13, no. 1)
    Brizalina striatula (Cushman, 1922) CPC 27386 (Fig. 13, no. 3)

Family: Buliminidae Jones, 1875
Genus: *Bulimina* d'Orbigny, 1826
    Bulimina elongata subulata (Cushman & Parker, 1937) (Fig. 13, no. 17)
    Bulimina marginata (d'Orbigny, 1826) CPC 27388 (Fig. 13, no. 18)
Genus: *Reussella* Galloway, 1933
    Reussella spinulosa (Reuss, 1850) CPC 27389 (Fig. 13, no. 12)

Fig. 15. **1,** *Uvigerina* cf. *peregrina* Sample Y19, tidal channel. x60 Lateral view; **2-3,** *Angulodiscorbis quadrangularis* Sample Y52, Windang Island. x93 Lateral and umbilical views; **4,** *Patellinella inconspicua* Sample Y42, Windang Island. x105 Umbilical and lateral views; **5-7,** *Buccella pustulosa* Sample Y52, Windang Island. x115 Apertural, umbilical and spiral views; **8-9,** *Rosalina anglica* Sample Y52, Windang Island. x48 Spiral and umbilical views; **10,** *Amphicoryna scalaris* Sample Y19, tidal channel. x60 Lateral view; **11-14,** *Rosalina bradyi* Sample Y52, Windang Island. x63 Umbilical, spiral, apertural and floating chamber views; **15,** *Rosalina australis* Sample Y52, Windang Island. x65 Spiral view; **16-18,** *Glabratella pulvinata* Sample Y52, Windang Island. x93 Spiral, lateral and umbilical views; **19-20,** *Cymbaloporetta bradyi* Sample Y52, Windang Island. x43 Umbilical and spiral views; **21-23,** *Glabratella* sp. II Sample Y19, tidal channel. x86 Spiral and umbilical views; **24-25,** *Planulinoides biconcavus* Sample 282, tidal channel. x65 Spiral and apertural views.

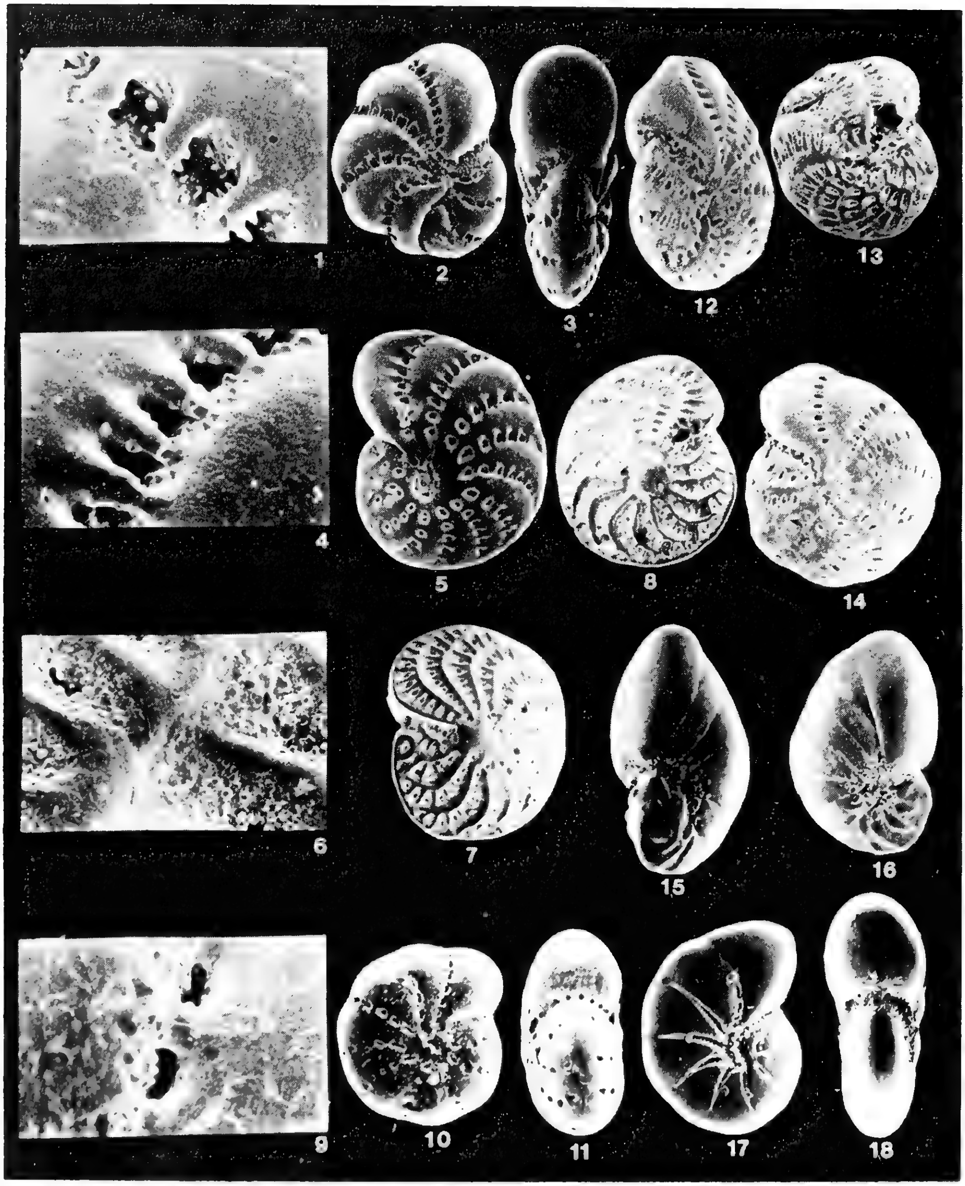


Fig. 16. **1-3,** *Elphidium depressulum* Sample Y52, Windang Island. Details of lateral process (x460), umbilical and apertural views (x80); **4-5,** *Elphidium advenum* Sample Y42, Windang Island. Details of lateral process (x460), and umbilical view (x87); **6-8,** *Elphidium macellum* Sample Y42, Windang Island. Details of lateral process (x460), and spiral view (x60); **9-11,** *Cribrononion sydneyensis* Sample 390, Lake Illawarra. Details of lateral process (x460), and spiral and apertural views (x50); **12-14,** *Elphidium argenteus* Sample Y52, Windang Island. x52 Lateral-apertural and umbilical views; **15-16,** *Nonionella auris* Sample Y19, tidal channel. x72 Lateral-apertural and umbilical views; **17-18,** *Nonion depressulus* Sample Y19, tidal channel. x87 Umbilical and apertural views

Family: Turrilinidae Cushman, 1927
  Genus: *Buliminoides* Cushman, 1911
    Buliminoides gracilis (Collins, 1953) CPC 27391 (Fig. 13, no. 7)
    Buliminoides williamsonianus (Brady, 1881) CPC 27392 (Fig. 13, no. 8)

Family: Uvigerinidae Haeckel, 1894
  Genus: *Uvigerina* d'Orbigny, 1826
    Uvigerina bassensis (Parr, 1950) CPC 27395 (Fig. 13, no. 5)
    Uvigerina sp. cf. *peregrina* (Cushman, 1923) (Fig. 15, no. 1)

Family: Glabratellidae Loeblich & Tappan, 1963
  Genus: *Angulodiscorbis* Uchio, 1953
    Angulodiscorbis quadrangularis (Uchio, 1953) CPC 27396 (Fig. 15, nos 2-3)
  Genus: *Glabratella* Dorreen, 1948
    Glabratella australensis (Heron-Allen & Earland, 1932) CPC 27397 (Fig. 14, nos 17-20)
    Glabratella sp. cf. *parri* (Collins, 1974)
    Glabratella patelliformis (Brady, 1884) CPC 27398
    Glabratella pulvinata (Brady, 1884) CPC 27399 (Fig. 15, nos 16-18)
    Glabratella tabernacularis (Brady, 1884) CPC 27400 (Fig. 14, nos 15-16)
    Glabratella sp. I CPC 27401 (Fig. 14, nos 21-22)
    Glabratella sp. II CPC 27402 (Fig. 15, nos 21-23)

Family: Discorbidae Ehrenberg, 1838
  Genus: *Baggina* Cushman, 1926
    Baggina phillippinensis (Cushman, 1921) CPC 27403 (Fig. 17, nos 18-19)
  Genus: *Buccella* Andersen, 1952
    Buccella pustulosa (Albani, 1982) CPC 27404 (Fig. 15, nos 5-7)
  Genus: *Discorbinella* Bandy, 1949
    Discorbinella bertheloti (d'Orbigny, 1839) CPC 27405 (Fig. 18, nos 13-14)
    Discorbinella planoconcava (Chapman, Parr & Collins, 1932) CPC 27406 (Fig. 18, no. 25)
  Genus: *Lamellodiscorbis* Bermudez, 1952
    Lamellodiscorbis dimidiatus (Jones & Parker, 1862) CPC 27407 (Fig. 17,nos 9-11)
  Genus: *Patellinella* Cushman, 1928
    Patellinella inconspicua (Brady, 1884) CPC 27408 (Fig. 15, no. 4)
  Genus: *Planulinoides* Parr, 1941
    Planulinoides biconcavus (Jones & Parker, 1862) CPC 27409 (Fig. 15, nos 24-25)

Family: Rosalinidae Reiss, 1963
  Genus: *Rosalina* d'Orbigny, 1826
    Rosalina anglica (Cushman, 1931) CPC 27410 (Fig. 15, nos 8-9)
    Rosalina australis (Parr, 1932) CPC 27411 (Fig. 15, no. 15)
    Rosalina bradyi (Cushman, 1951) CPC 27412 (Fig. 15, nos 11-14)

Family: Robertinidae Reuss, 1850
  Genus: *Lamarckina* Berthelin, 1881
    Lamarckina sp. CPC 27413 (Fig. 14, nos 11-12)

Family: Cymbaloporidae Cushman, 1927
  Genus: *Cymbaloporetta* Cushamn, 1928
  Cymbaloporetta bradyi (Cushman, 1915) CPC 27414 & 27415 (Fig. 15, nos 19-20)

Family: Planorbulinidae Schwager, 1877
  Genus: *Acervulina* Schultz, 1854
    Acervulina inhaerens (Schultze, 1854) CPC 27416 & 27417 (Fig. 17, nos 14-15)
  Genus: *Planorbulina* d'Orbigny, 1826
    Planorbulina mediterranensis (d'Orbigny, 1826) CPC 27418 (Fig. 17, no. 12)

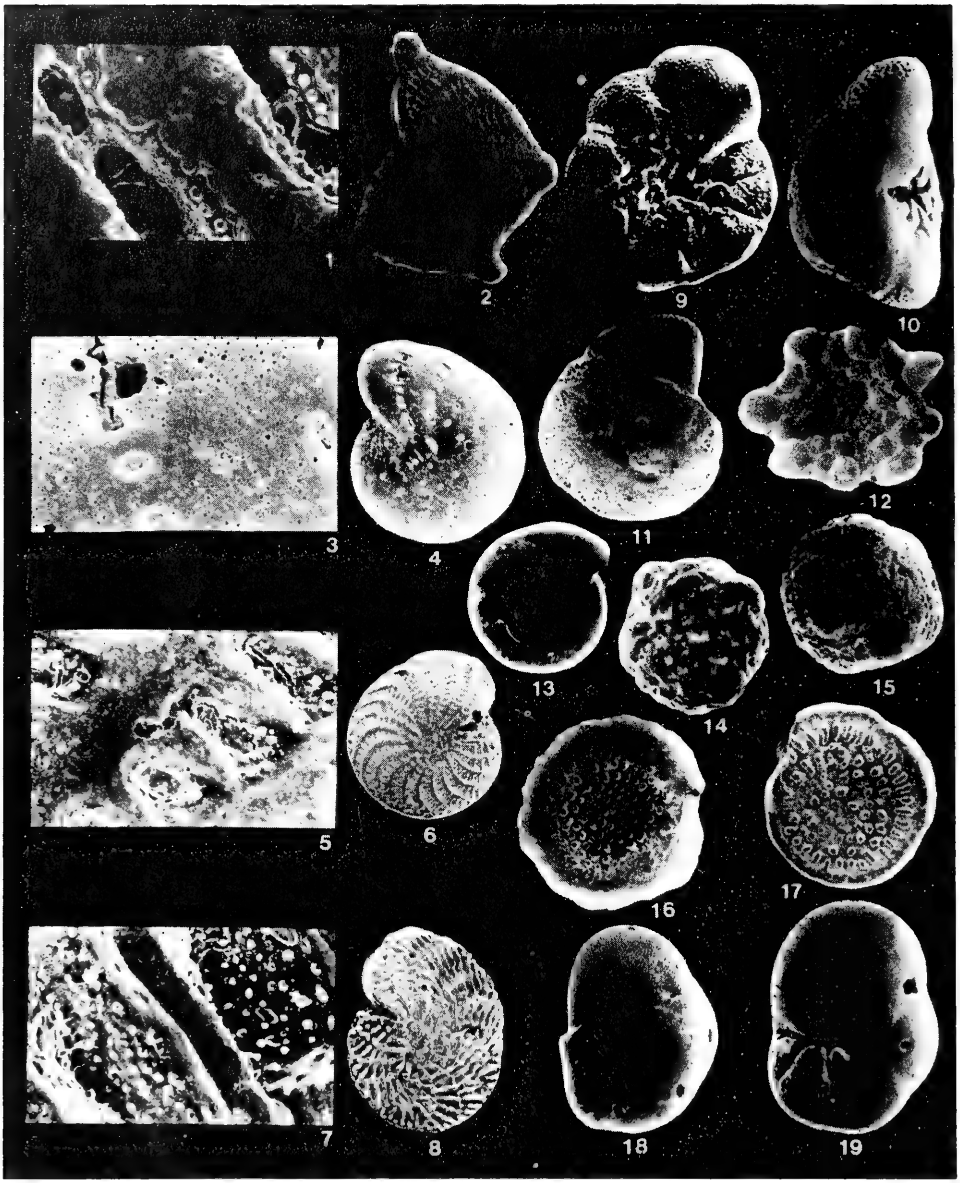


Fig. 17. **1-2,** *Parrellina imperatrix* Sample Y42, Windang Island. Details of lateral process (x460), and spiral view (x20); **3-4,** *Elphidium* sp. Sample Y19, tidal channel. Details of lateral process (x460), and spiral view (x91); **5-6,** *Elphidium crispum* Sample 282, tidal channel. Details of lateral process (x460), and spiral view (x31); **7-8,** *Elphidium jenseni* Sample 282, tidal channel. Details of lateral process (x460), and spiral view (x20); **9-11,** *Lamellodiscorbis dimidiatus* Sample Y52, Windang Island. x26 Umbilical, lateral-apertural and spiral views; **12,** *Planorbulina mediterranensis* Sample Y18, tidal channel. x27 Spiral view; **13,** *Spirillina vivipara* Sample 282, tidal channel. x86 Spiral view; **14-15,** *Acervulina inhaerens* Sample Y52, Windang Island. x63 Umbilical and spiral views; **16,** *Spirillina tuberculata* Sample Y19, tidal channel. x55 Umbilical view; **17,** *Spirillina* sp. Sample Y19, tidal channel. x95 Umbilical view; **18-19,** *Baggina phillippinensis* Sample Y52, Windang Island. x52 Spiral and umbilical views.

Family: Elphidiidae Galloway, 1933
  Genus: *Cribrononion* Thalmann, 1947
    Cribrononion sydneyensis (Albani, 1978) CPC 27424 (Fig. 16, nos 9-11)
  Genus: *Elphidium* Montfort, 1808
    Elphidium advenum (Cushman, 1922) CPC 27425 (Fig. 16, nos 4-5)
    Elphidium argenteus (Parr, 1945) CPC 27426 (Fig. 16, nos 12-14)
    Elphidium crispum (Linne, 1758) CPC 27427 (Fig. 17, nos 5-6)
    Elphidium depressulum (Cushman, 1933) (Fig. 16, nos 1-3)
    Elphidium jenseni (Cushman, 1924) CPC 27428 (Fig. 17, nos 7-8)
    Elphidium macellum (Fichtel & Moll, 1798) CPC 27429 (Fig. 16, nos 6-8)
    Elphidium sp. CPC 27430 (Fig. 17, nos 3-4)
  Genus: *Parrellina* Phalmann, 1951
    Parrellina imperatrix (Brady, 1881) CPC 27431 (Fig. 17, nos 1-2)

Family: Nonionidae Schultze, 1854
  Genus: *Nonion* Montfort, 1808
    Nonion depressulus (Walker & Jacob, 1798) (Fig. 16, nos 17-18)
  Genus: *Nonionella* Cushman, 1926
    Nonionella auris (d'Orbigny, 1839) CPC 27434 (Fig. 16, nos 15-16)

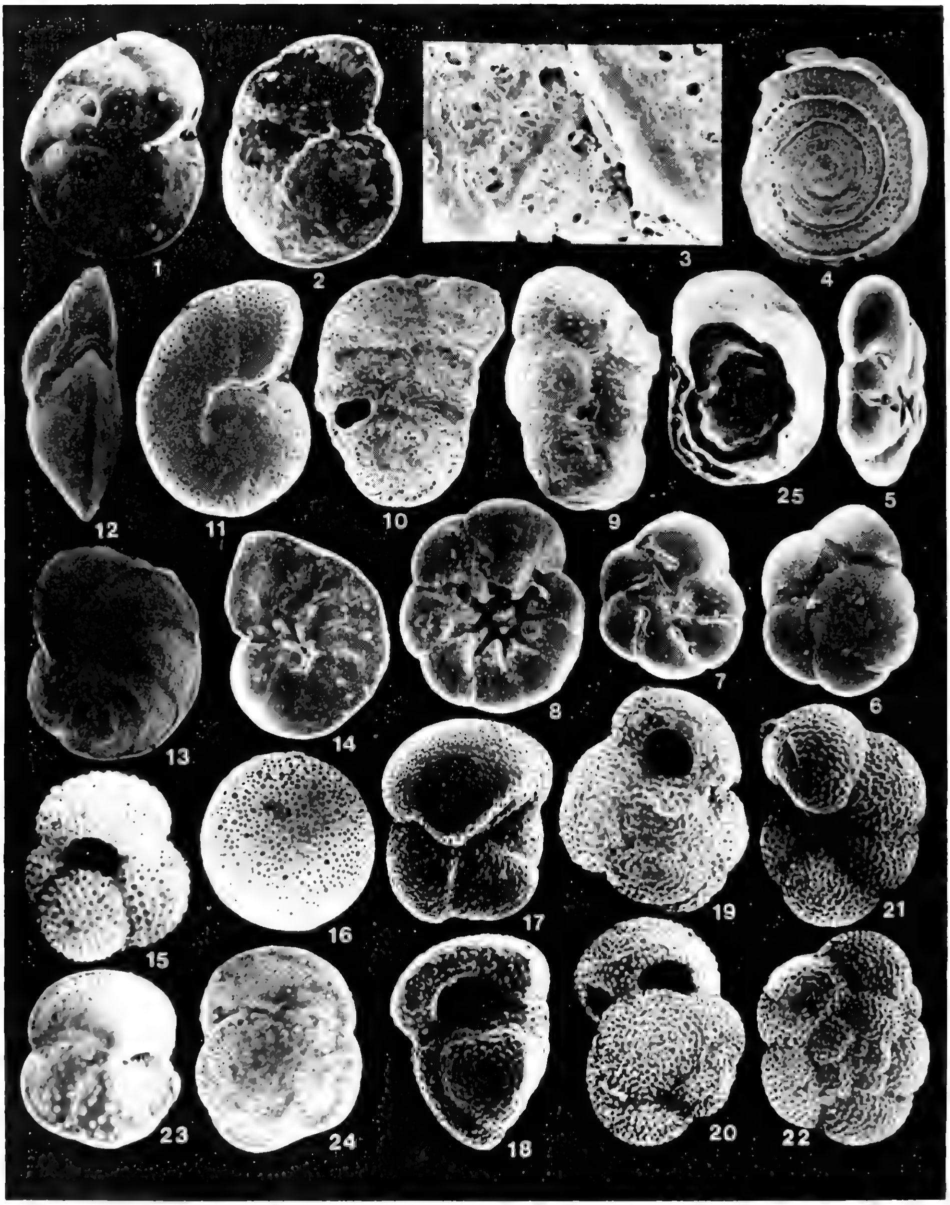
Family: Rotaliidae Ehrenberg, 1839
  Genus: *Ammonia* Brünnich, 1772
    Ammonia beccarii (Linné, 1767) CPC 27432 (Fig. 18, no. 8)
  Genus: *Rotalia* Lamarck, 1804
    Rotalia perlucida (Heron-Allen & Earland, 1913) CPC 27433 (Fig. 18, nos 5-7)

Family: Cibicididae Cushman, 1927
  Genus: *Cibicides* Montfort, 1808
    Cibicides cygnorum (Carter, 1964) CPC 27419 (Fig. 18, nos 1-2, 12)
    Cibicides refulgens (Montfort, 1808) CPC 27420
  Genus: *Dyocibicides* Cushman & Valentine, 1930
    Dyocibicides biserialis (Cushman & Valentine, 1930) CPC 27421 (Fig. 18, nos 9-10)

Family: Anomalinidae Cushman, 1927
  Genus: *Anomalina* d'Orbigny, 1826
    Anomalina nonionoides (Parr, 1932) CPC 27435 (Fig. 18, no. 11)

Family: Spirillinidae Reuss, 1862
  Genus: *Patellina* Williamson, 1858
    Patellina corrugata (Williamson, 1858) CPC 27436 (Fig. 14, nos 13-14)
  Genus: *Spirillina* Ehrenberg, 1843
    Spirillina denticulata (Brady, 1884) CPC 27437 (Fig. 18, nos 3-4)
    Spirillina inaequalis (Brady, 1879) CPC 27438
    Spirillina tuberculata (Brady, 1884) CPC 27439 (Fig. 17, no. 16)
    Spirillina vivipara (Ehrenberg, 1843) CPC 27440 (Fig. 17, no. 13)
    Spirillina sp. CPC 27441 (Fig. 17, no. 17)

Family: Globigerinidae d'Orbigny, 1826
  Genus: *Globigerina* d'Orbigny, 1826
    Globigerina bulloides (d'Orbigny, 1826) CPC 27442 (Fig. 18, no. 15)
    Globigerina sp.
  Genus: *Globigerinoides* Cushman, 1927
    Globigerinoides ruber (d'Orbigny, 1839) CPC 27443 (Fig. 18, nos 19-20)
  Genus: *Globoquadrina* Finlay, 1947
    Globoquadrina dutertrei (d'Orbigny, 1839) CPC 27444 (Fig. 18, nos 21-22)
  Genus: *Orbulina* d'Orbigny, *in* de la Sagra, 1839
    Orbulina universa (d'Orbigny, 1839) CPC 27445 (Fig. 18, no. 16)
  Genus: *Pulleniatina* Cushman, 1927
    Pulleniatina obliqueloculata (Parker & Jones, 1865)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Family: Globorotaliidae Cushman, 1927
Genus: *Globorotalia* Cushman, 1927
Globorotalia hirsuta (d'Orbigny, 1839) CPC 27446 (Fig. 18, nos 23-24)
Subgenus: *Turborotalia* Cushman & Bermudez, 1949
Globorotalia (Turborotalia) inflata (d'Orbigny, 1839) CPC 27447 (Fig. 18, nos 17-18)

Fig. 18. **1-2, 12,** *Cibicides cygnorum* Sample 282, tidal channel. x78 Umbilical, spiral and apertural views; **3-4,** *Spirillina denticulata* Sample Y19, tidal channel. Details of ornamentation (x460), and spiral view (x74); **5-7,** *Rotalia perlucida* Sample Y52, Windang Island. x70 Apertural, spiral and umbilical views; **8,** *Ammonia beccarii* Sample Y10, Lake Illawarra. x43 Umbilical view; **9-10,** *Dyocibicides biserialis* Sample Y42, Windang Island. x43 Umbilical and spiral views; **11,** *Anomalina nonionoides* Sample Y19, tidal channel. x50 Spiral view; **13-14,** *Discorbinella bertheloti* Sample Y19, tidal channel. x87 Spiral and umbilical views; **15,** *Globigerina bulloides* Sample Y19, tidal channel. x71 Umbilical view; **16,** *Orbulina universa* Sample Y19, tidal channel. x64; **17-18,** *Globorotalia (Turborotalia) inflata* Sample 282, tidal channel. x71 Umbilical and apertural views; **19-20,** *Globigerinoides ruber* Sample Y19, tidal channel. x72 Spiral, lateral-apertural views; **21-22,** *Globoquadrina dutertrei* Sample Y19, tidal channel. x70 Umbilical and spiral views; **23-24,** *Globorotalia hirsuta* Sample Y19, tidal channel. x70 Umbilical and spiral views; **25,** *Discorbinella planoconcava* Sample Y42, Windang Island. x90 Umbilical view.

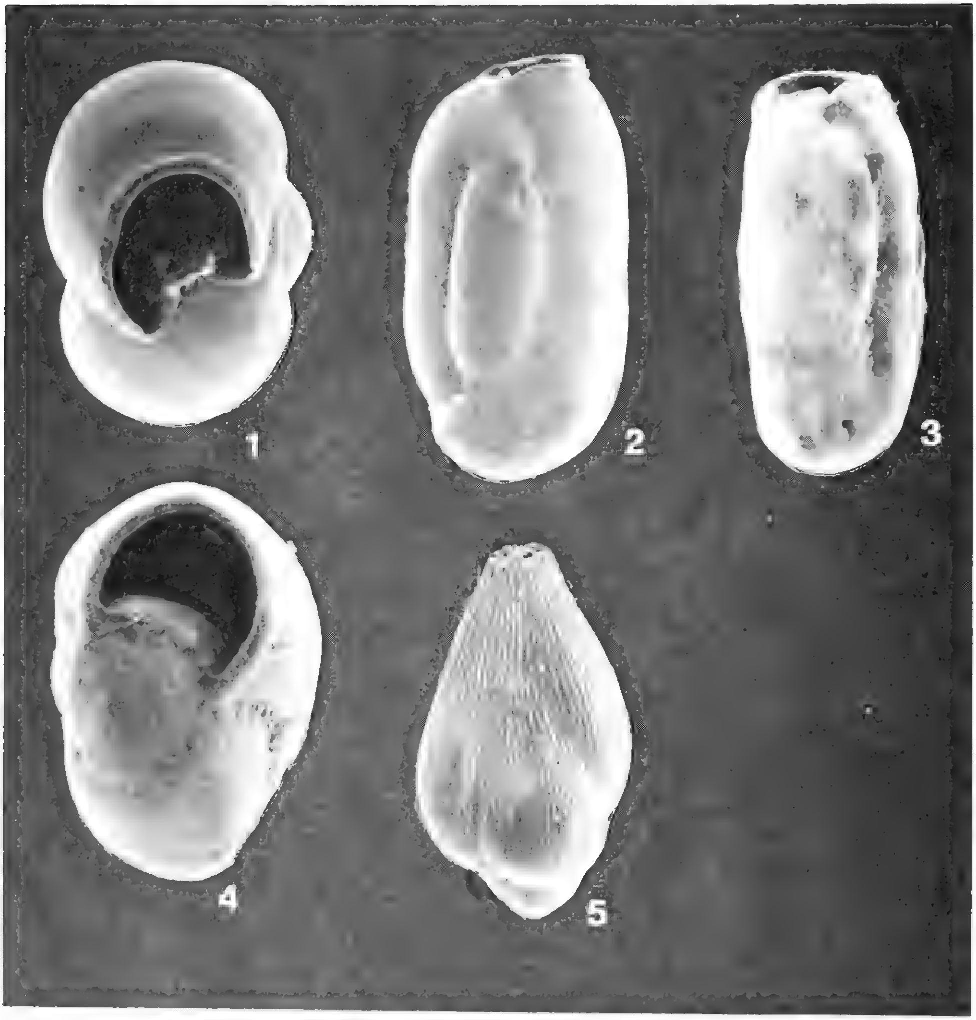

Fig. 19. **1-4**, *Miliolinella subrotunda* Sample Y28, Lake Illawarra. 1, 4 apertural views (x200); 2 spiral view (x170); 3 lateral view (x160); **5**, *Guttulina regina* Sample Y42, Windang Island. x60 Lateral view.

Status of the Genera *Ophiopeza* and *Ophiopsammus* (Echinodermata: Ophiuroidea) in Australian Waters, with the Description of a new Species

L. L. VAIL and F. W. E. ROWE

VAIL, L. L., & ROWE, F. W. E. Status of the genera *Ophiopeza* and *Ophiopsammus* (Echinodermata: Ophiuroidea) in Australian waters, with the description of a new species. *Proc. Linn. Soc. N.S.W.* 110(3), (1988) 1989: 267-288.

A study of type and other material has resulted in a reappraisal of the generic limits of the ophiodermatid genera *Ophiopeza* Peters, 1851 and *Ophiopsammus* Lütken, 1869. By using disc scaling as a character of generic significance the species *fallax arabica* A. M. Clark, 1968, *cylindrica* Hutton, 1872a, and *spinosa*, Ljungman, 1867, have been retained in the genus *Ophiopeza*, type-species *fallax fallax* Peters, 1851, while the species *aequalis* Lyman, 1880, *anchista* H. L. Clark, 1911, *assimilis* Bell, 1888, and *maculata* Verrill, 1869 have been transferred to the genus *Ophiopsammus*, type-species *yoldii* Lütken, 1856. In addition, *Ophiopsammus angusta* sp. nov. is described from southeastern Australian waters. The following species have been synonymized: *Ophiopeza arenosa* (Lyman, 1879) and *Ophiopeza gracilis* (Mortensen, 1924) with *Ophiopeza cylindrica*; *Ophiopeza dubiosa* (de Loriol, 1893) with *Ophiopeza spinosa*; and *Ophiopeza dyscrita* (H. L. Clark, 1909) and *Ophiopeza nigra* (H. L. Clark, 1938) with *Ophiopsammus assimilis*. *Ophiopsammus aequalis* is recorded for the first time from Australia. Notes are given for a misidentified type specimen of *anchista*. A key to all the known species of *Ophiopeza* and *Ophiopsammus* is given, except for *exilis* Koehler, 1905.

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INTRODUCTION

The taxonomic status of *Pectinura* Forbes 1843, *Ophiopeza* Peters 1851, and *Ophiopsammus* Lütken 1869 has been most recently discussed by A. M. Clark (1968). Briefly, *Pectinura* was described by Forbes (1843) for *vestita* from a small specimen taken off southern Turkey. *Ophiopeza* was described by Peters (1851) for the species *fallax* which was collected off Mozambique. These two genera were separated on the presence of supplementary oral shields in *Pectinura* and their absence in *Ophiopeza*. *Ophiopsammus* was established by Lütken (1869) for his earlier described species *Ophiopeza yoldii*. This genus was distinguished by the absence of supplementary oral shields and the concealment of radial shields by disc granules. Lyman (1882) subsequently referred *yoldii* back to *Ophiopeza* although he gave no justification. He listed 12 species belonging to the genus *Pectinura* and five species to *Ophiopeza*. In a review, H. L. Clark (1909a) synonymized both *Ophiopeza* and *Ophiopsammus* with *Pectinura* on the grounds that the presence or absence of supplementary oral shields in these genera lacked sufficient taxonomic value. However, he stated that if his interpretation of Forbes' inadequate description of *vestita* was incorrect then *Pectinura* should probably replace *Ophiarachnella* Ljungman, 1871. Furthermore, *Ophiopeza* would become the available generic name for the 10 species he included in the genus *Pectinura*. Later in the same year, he described (H. L. Clark, 1909b) another species of *Pectinura*, *dyscrita*, from off New South Wales. During his visits to Australia in 1913, 1929, and 1932, H. L. Clark collected only one specimen of *Pectinura* which he described as a new species, *nigra* (H. L. Clark, 1938) from Western Australia. In his 1946 review of the Australian echinoderm fauna, H. L. Clark recorded five species of

Pectinura from Australian waters, mentioning that none was known from adequate material.

Mortensen (1940) recorded *Ophiopeza fallax* from the Iranian Gulf. He questioned whether the species should be referred to the genus *Pectinura* but decided that since the type-species of *Pectinura*, *P. vestita*, is insufficiently known he preferred to use the name *Ophiopeza*. A. M. Clark (1968) discussed the problem of these genera and concurred with Mortensen's use of the name *Ophiopeza*, especially since the holotype of *Pectinura* is now lost. She suggested that *P. vestita* could have been a specimen of the Mediterranean species *Ophioconis forbesi* which had lost disc granules from the oral shields. However, A. M. Clark (1968) did not agree with Lyman's inclusion of *Ophiopsammus* in the synonymy of *Ophiopeza* and, on the basis of the shape of its dorsal arm plates, she revived the generic name *Ophiopsammus* for the species *yoldii*.

During the course of researching the echinoderm fauna of New South Wales (F.W.E.R.; ARGS D1805325; MST 84/2092) extensive collections made along the coast during 1981 and 1982 by staff of the Echinoderm Section of the Australian Museum yielded a large number of specimens referred to the genus *Ophiopeza*, as understood by A. M. Clark (1968). This material has been compared with other specimens in the collections of the Australian Museum and with type and other specimens borrowed from the British Museum (Natural History), Museum of Comparative Zoology, Museum of Victoria, National Museum of New Zealand, and the US National Museum (Smithsonian). As a result of our investigations, we have been able to clarify the status of the species of *Ophiopeza* and *Ophiopsammus* occurring in Australia, as well as describing a new species and establishing a new record. Furthermore, we have established the value of disc scaling in separating the genera *Ophiopeza* and *Ophiopsammus*. With the exception of Lyman's (1882) use of this feature in a key to the species of *Pectinura*, disc scaling has been ignored in ophiodermatid taxonomy.

The following abbreviations have been used: ca = approximately; coll. = collection; d.d. = disc diameter; d.r. = disc radius; R = arm length from base of disc to arm tip; AM = Australian Museum, Sydney: BM(NH) = British Museum (Natural History), London; MCZ = Museum of Comparative Zoology, Cambridge, Mass.; NMNZ = National Museum of New Zealand, Wellington; MV = Museum of Victoria, Melbourne; USNM = US National Museum (Smithsonian), Washington; N.S.W. = New South Wales; N.Z. = New Zealand: Qld = Queensland; S.A. = South Australia; Tas. = Tasmania; Vic. = Victoria; W.A. = Western Australia.

All known species in each of the genera (except for *Ophiopeza exilis*) are included in their respective keys, but only species known from Australian waters are discussed in detail.

SYSTEMATIC ACCOUNT

Family OPHIODERMATIDAE

Genus ***Ophiopeza*** Peters

Ophiopeza Peters, 1851: 465 (type-species *O. fallax* Peters, 1851, by monotypy).

Ophiopezella Ljungman, 1872: 639 (type-species *Ophiarachna spinosa* Ljungman, 1867, by monotypy).

Pectinura: autorum [non *Pectinura* Forbes, 1843].

Diagnosis: A genus of ophiodermatid with radial shields usually obscured by granules; marginal disc scales enlarged, usually covered by granules, rarely bare; disc scales coarse, overlapping, 1-3 large scales separating the two plates of each pair of radial shields; oral plates covered by granules; oral shields naked, supplementary oral shields frequently present and at least partially naked; dorsal arm plates fan shaped to transversely rectangular (up to ca 2 x wider than long), flat; arm spines never exceeding one arm segment in length, often appressed.

Other species included: *O. fallax arabica* A. M. Clark, 1968; *O. cylindrica* (Hutton, 1872a); *O. spinosa* (Ljungman, 1867).

Remarks: We concur with Mortensen (1940) and A. M. Clark (1968) in their recognition of the genus *Ophiopeza*. Also, we are able to support A. M. Clark's reasoning and decision in her resurrection of the genus *Ophiopsammus* from synonymy with *Ophiopeza*. However, in addition, we draw attention to differences in the type of disc scaling between *Ophiopeza* and *Ophiopsammus* (see p. 268). Using these characters, we propose to restrict *Ophiopeza* for *fallax fallax*, *fallax arabica*, *cylindrica*, and *spinosa*. Of the other species previously referred to *Ophiopeza* by A. M. Clark (1968), we propose that *anchista* H. L. Clark, 1911, *assimilis* Bell, 1888, *aequalis* Lyman, 1880, and *maculata* Verrill, 1869, be referred to *Ophiopsammus*, as we consider them to be congeneric with *yoldii* Lütken, the type species of *Ophiopsammus*. We are uncertain of the affinity of *exilis* (Koehler, 1905) which A. M. Clark (1968) transferred back from *Pectinura* to *Ophiopeza* as its disc scaling is not evident on the figure given for it by Koehler (1905: pl. 2, fig. 5) and because we have not examined material referable to this species.

Ophiopeza cylindrica (Hutton, 1872a)
Figs 1**A-C**, 2**A-B**

Ophiura cylindrica Hutton, 1872a: 3; 1872b: 811.

Pectinura arenosa Lyman, 1879: 48, pl. 14, figs 392-394; 1882: 15, pl. 23, figs 10-12. H. L. Clark, 1909: 117; 1921: 141; 1946: 257. A. M. Clark, 1966: 327. Dartnall, 1980: 42, 71.

Ophiopeza cylindrica. Farquhar, 1895: 198, 1898b: 306 [? non *Ophiopeza cylindrica*. Farquhar, 1898a: 190, pl. 14, figs 4, 5 = *assimilis*.]

Pectinura cylindrica. H. L. Clark, 1909: 117; 1915: 303 [? non *Pectinura cylindrica*. Mortensen, 1924: 172, non fig. 35(1-2) = *assimilis*.]

Pectinura gracilis Mortensen, 1924: 173, figs 35(3-5), 36.

Ophiopeza arenosa. A. M. Clark, 1968: 313. Rowe and Vail, 1982: 222. [? non *Ophiopeza arenosa*. Baker, 1982: 431, fig. 10.18c. = *assimilis*.]

Material examined: Lectotype of *O. cylindrica* NMNZ Ech 6, no coll. data; **lectotype** of *O. gracilis* NMNZ Ech 375, Paterson Inlet, Stewart Id, N.Z., 9-28m, 17. xi. 14; **holotype** of *O. arenosa* BM(NH) 82.12.23.247, off East Mancoeur Id, Bass Strait, Tas., 70-74m, 2.iv.1874; 1 **paratype** of *O. arenosa* BM(NH) 82.12.23.247 (pt) off East Mancoeur Id, Bass Strait, Tas., 70-74m, 2.iv.1874; 1 spec., AM G7831, Watson's Bay, Port Jackson, N.S.W., no coll. depth or date; 1 spec., AM G11413, Broughton Id, nr Port Stephens, N.S.W., 66m, no coll. date; 2 spec., AM J15049, NW Solitary Id, nr Coffs Hbr, N.S.W., 22m, 10.ii.82; 1 spec., AM G11032, Port Jackson, N.S.W., no coll. depth; 1 spec., AM J1974, Port Phillip, Vic., no coll. depth; 3 spec., MNMZ (Ech 3412), Paterson Inlet, N.Z., 23m, 26.i.60; 2 spec., NMNZ (ECH 3413), North Arm, Port Pegasus, Stewart Id, N.Z. 37-44m, 22.ii.72.

Diagnosis: Disc diameter to 11mm, densely covered with round granules, 13-16 per mm; coarse, slightly overlapping scales underlying the granules. Each interradius with 7-9 marginal disc plates, middle ones largest, each plate obscured by granule cover. Radial

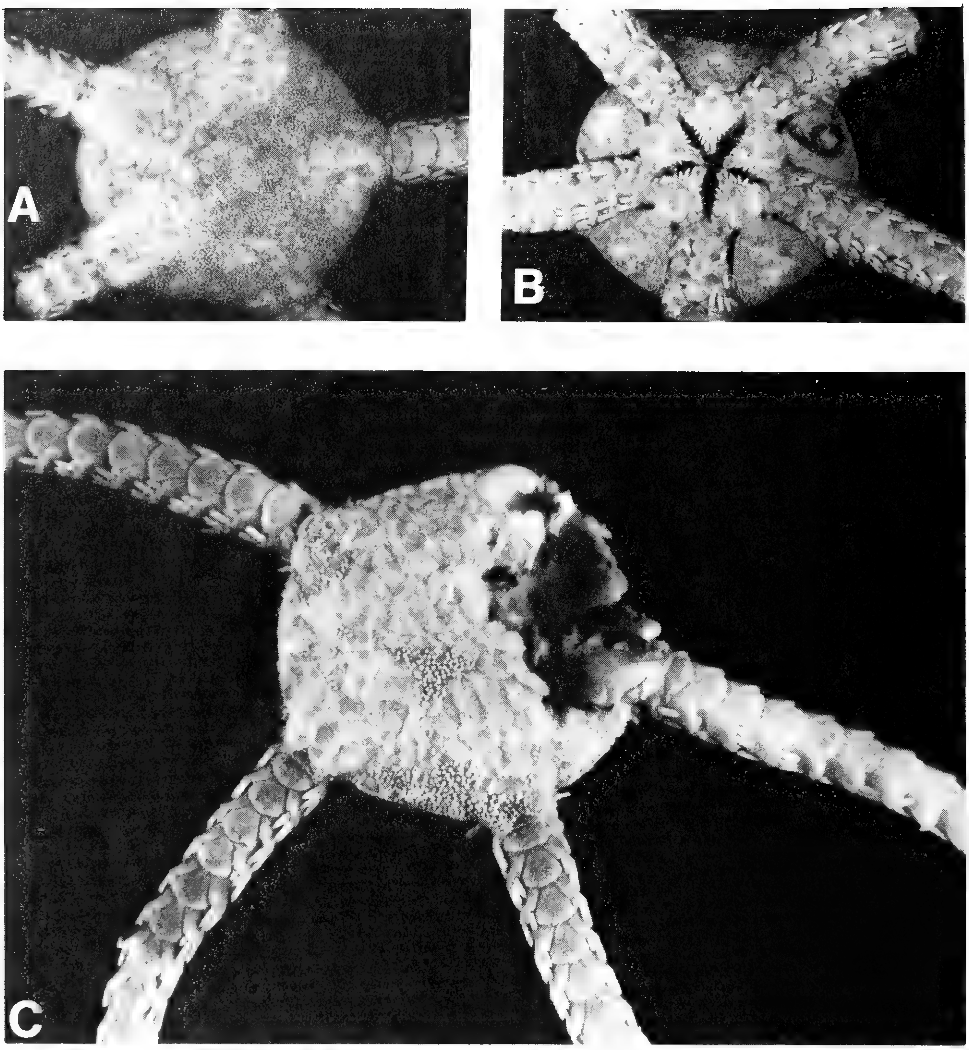

Fig. 1. **A**, **B**, *Ophiopeza cylindrica*, lectotype (NMNZ Ech 6), dorsal and ventral view respectively, dd = 8mm. **C**, *Ophiopeza gracilis*, lectotype (NMNZ Ech 375), doral view, dd = 5mm. Some disc granules were removed in **A** and **C** to show disc scaling.

shields 0.1 x d.r., obscured by granules. Three conspicuous plates in triangular arrangement separating the two plates of each pair of radial shields. Arms to 42mm, 2.6-3.9 x d.d., dorsal plates fan shaped in specimens with d.d. $\overset{\sim}{<}$ 7mm becoming transversely rectangular in shape (up to 2.0 times wider than long) in larger specimens; ventral plates as long as or slightly longer than wide. Eight to ten short, stout arm spines per segment; lowermost sometimes longer and wider than the others, which were about half an arm segment long. Two tentacle scales per pore, inner one longest, the outer one covering the base of lowest arm spine. Oral shields usually with a distal supplementary plate which is up to ½ as long as the oral plate; adoral plates roughly triangular in shape. Oral plates covered with granules. Seven to eight short, flat, oral papillae; tooth papillae flattish, rounded distally.

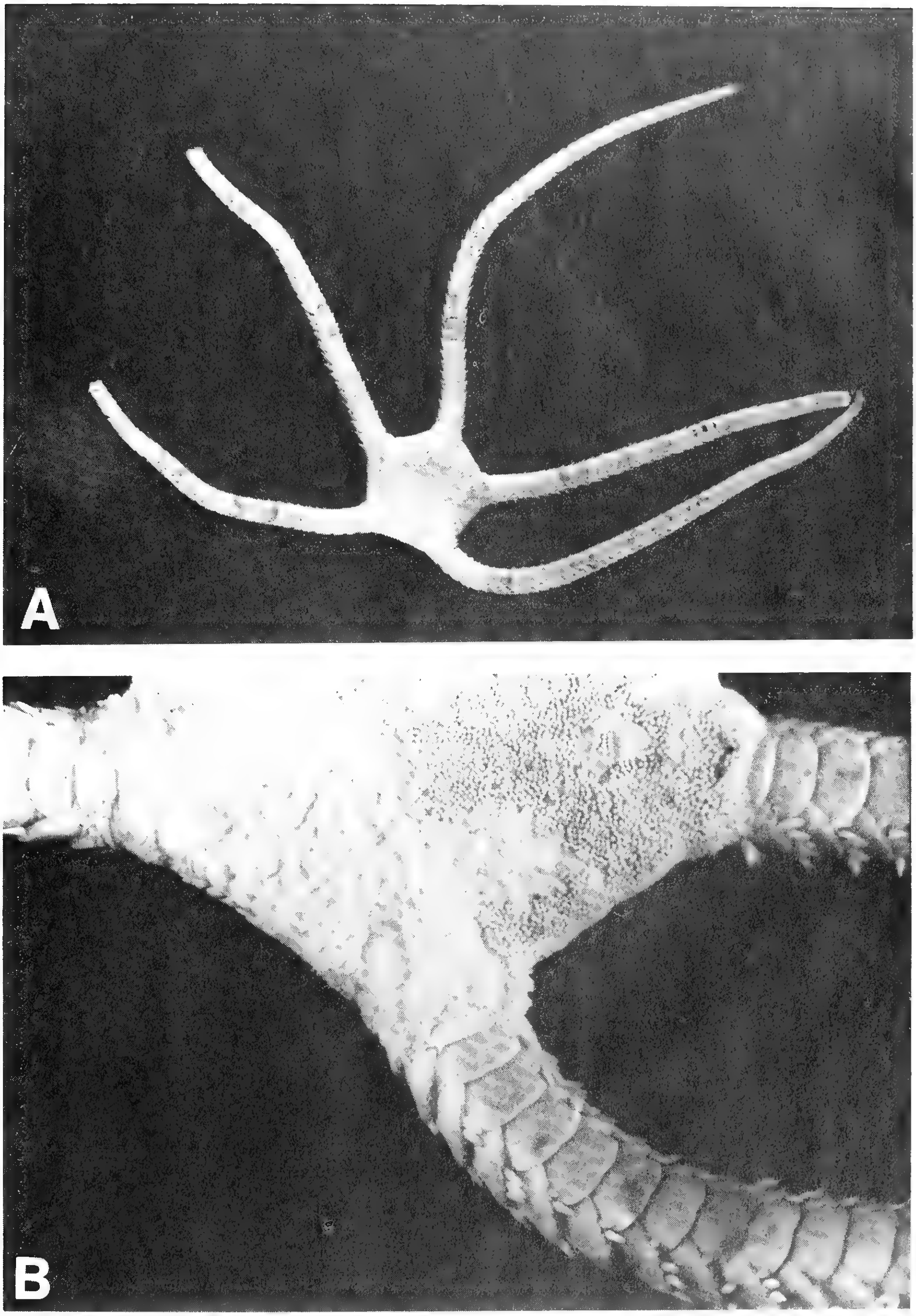

Fig. 2. **A**, **B**, *Ophiopeza arenosa*, paratype (BM(NH) 82.12.23.247 (pt)), dorsal view, dd = 9mm. Synonymized with *Ophiopeza cylindrica* herein. Some disc granules were removed to show disc scaling.

Colour (dried): Light brown to charcoal grey; some arms with dark, cream, or reddish bands.

Distribution: Northeastern Tas. and Port Phillip Bay, Vic. to off Coffs Harbour, N.S.W., Stewart Id, N.Z.; to 74m.

Remarks: The description of *Ophiura cylindrica* by Hutton (1872a) was based on two specimens (Hutton, 1872b); neither of which had locality data according to the original authority. Lyman (1882) synonymized this species with *Pectinura rigida* Lyman, 1874, although he gave no reasons for the synonymy. Farquhar (1895) compared Lyman's description of *P. rigida* with the syntype series of *O. cylindrica* and concluded that they represented two distinct species. H. L. Clark (1915) subsequently synonymized *rigida* with *Ophiarachnella septemspinosa* (Müller and Troschel, 1842). Farquhar (1898a) described and figured material as *cylindrica*, which we believe refers to *Ophiopsammus assimilis* on the grounds of dorsal arm plate shape (see below). One of two syntypes of *O. cylindrica* was already lost when Mortensen (1924) compared this species with his newly-established species, *Ophiopeza gracilis*. We have examined the remaining syntype specimen of *O. cylindrica* (NMNZ Ech 6) examined by Mortensen, and agree with his comments (Mortensen, 1924). We are therefore convinced that this is one of Hutton's syntype series and we designate it as the **lectotype** of *O. cylindrica*.

O. gracilis (Mortensen, 1924) was established on a number of specimens from New Zealand. These included an unspecified number from Stewart Id, two from Queen Charlotte Sound, and one from Three Kings Island. We designate one specimen from Stewart Id (NMNZ Ech 375) as a **lectotype** of *O. gracilis* (Mortensen) since we consider it to be part of his syntype series.

When Mortensen described *O. gracilis*, he compared it with the closely related species *cylindrica* and also figured each of the species (Mortensen, 1924: 174, fig. 35 (1-2)). We have material of a size similar to the specimens of *cylindrica* figured by both Mortensen (1924) and Farquhar (1898a: 190, pl. 14, figs 4, 5). Our material agrees with the specimens figured by both of them although we identify our specimens as *Ophiopsammus assimilis* on the basis of disc scaling and shape of the dorsal arm plates. Consequently, we contend that Mortensen and Farquhar mistakenly referred specimens of *assimilis* to *cylindrica*. However, we agree with the differences discussed by Mortensen (1924) between the species '*cylindrica*' and *gracilis* but only in that they refer to differences between *Ophiopsammus assimilis* (i.e. Mortensen's and Farquhar's *cylindrica*) and *cylindrica* s.s. (i.e. Mortensen's *gracilis*).

Mortensen (1924) used dorsal arm plate and arm spine shape, relative size of oral shields, and the extent of granulation on oral plates to differentiate '*cylindrica*' and *gracilis*. He concluded that the dorsal arm plates were basically fan shaped in *gracilis* but that they were more transversely rectangular in '*cylindrica*'. Table 1 summarizes measurements from 15 specimens we have identified as *cylindrica* s.s., based primarily on dorsal disc scaling. Dorsal arm plates change from fan shaped in small individuals (d.d. $\lesssim$ 7mm) to more transversely rectangular shaped in larger individuals, as shown in the dorsal arm plate ratio column of Table 1. This evidence suggests that the differences referred to by Mortensen can be explained by ontogenic development.

Ophiopeza arenosa was established on 6 type specimens by Lyman (1879). We have examined the holotype and a paratype (BM(NH) 82.12.23.247). Type material of *arenosa* was compared with the lectotype of *Ophiopeza cylindrica*. In these specimens, only slight differences attributable to size could be detected and these are within the range of variation found in *cylindrica* (Table 1).

TABLE 1

Measurements of specimens of Ophiopeza cylindrica

Registration no.	d.d.	d.a.p.r.	o.s.r.	n.s.p.	o.p.g.		
					$\bar{x}$	sd	n
NMNZ Ech 375	5	4.0	0.1	1	33	5.8	5
NMNZ Ech 3412	5	3.0	0.1	4	38*	—	1
NMNZ Ech 3412a	5	2.2	0.2	4	34	6.8	5
NMNZ Ech 3412b	7	2.0	0.1	2	41	2.7	5
AM J1974	7	1.8	0.1	5	34	3.5	5
AM G7831	7	1.8	0.1	5	48	4.2	4
NMNZ Ech 6	8	1.8	0.1	4	31	4.4	5
BM (NH) 82.12.23.247 (pt)	9	1.3	0.1	5	57*	—	1
AM G11413	9	1.8	0.1	5	?		
AM G11032	9	1.5	0.1	5	57*	—	1
NMNZ Ech 3413	10	1.7	0.1	5	72	10.1	5
BM (NH) 82.12.23.247	10	1.6	0.09	5	?		
AM J15049	10	1.6	0.09	5	56	3.6	5
NMNZ Ech 3413a	11	1.5	0.1	5	72	10.2	5
AM J15049	11	1.5	0.08	5	56	3.6	5

Abbreviations: d.d., disc diameter; d.a.p.r., dorsal arm plate ratio; o.s.r., oral shield ratio; n.s.p., number supplementary oral plates (maximum available is 5); o.p.g., oral plate granules with mean ($\bar{x}$), standard deviation (sd) and number (n) indicated; *, number of granules was estimated due to some missing granules; ?, all oral plate granules were missing (presumably either worn away or dislodged after preservation). Dorsal arm plate ratio was calculated for the fifth dorsal arm plate along the arm. This ratio is an approximate measure of the relative width of that plate's distalmost margin to its proximalmost one. Oral shield ratio is the approximate length of an individual's oral shield plate relative to its disc diameter. Bold registration numbers indicate type specimens.

After comparing the lectotype of *Ophiopeza cylindrica*, the lectotype of *Ophiopeza gracilis*, the holotype and paratype of *Ophiopeza arenosa* and 11 other specimens from New Zealand and Australia, we conclude that they are conspecific and that their variation in morphology is primarily due to ontogeny. *Ophiopeza arenosa* and *gracilis* are consequently synonymized with *Ophiopeza cylindrica.*

O. cylindrica has only been recorded from temperate seas whereas *O. spinosa*, *O. fallax fallax*, and *O. fallax arabica* are only known from tropical seas. In addition to their apparent geographic separation, *cylindrica* and *spinosa* differ most obviously by the fine, flat-topped granules of *spinosa* (see p. 275). *O. cylindrica* differs from *fallax fallax* and *fallax arabica* not only by the finer granulation of *cylindrica* but both *fallax* and *arabica* possess shorter arm spines, some bare marginal plates and, in *arabica*, bare radial shields.

Ophiopeza spinosa (Ljungman, 1867)
Fig. 3**A**,**B**

Ophiarachna spinosum Lungman, 1867: 305.

Ophiopeza fallax. Lütken, 1869: 35. [non *fallax* Peters, 1851.]

Pectinura spinosa. Lyman, 1874: 221.

Ophiopezella spinosa. Ljungman, 1872: 639. Lyman, 1882: 17. H. L. Clark, 1909a: 120; 1915: 304; 1921: 141, 1946: 258. Koehler, 1922: 338. Marsh and Marshall, 1983: 678.

Ophiopezella lütkeni de Loriol, 1893a: 392, pl. 13, fig. 1-1e.

Ophiopezella dubiosa de Loriol, 1893b: 7, pl. 23, fig. 2-2f. H. L. Clark, 1909a: 120. Koehler, 1922: 120.

Ophiopeza dubiosa. A. M. Clark, 1968: 313. Clark and Rowe, 1971: 127.

Ophiopeza spinosa. A. M. Clark, 1968: 313. Clark and Rowe, 1971: 90, 127, fig. 44e. Gibbs *et al.*, 1976: 130. Kingston, 1980: 145.

Material examined: (All specimens examined are held in the AM) 3 spec., J5352, Norwest Id, Capricorn Group, Qld, no coll. depth, vii.29; 3 spec., J5967, Norwest Id, Capricorn Group, Qld, no coll. depth or date; 2 spec., J8881, NW of Gillett Cay, Swain Reefs, Qld, no coll. depth, 17.x.62; 2 spec., J8882, off Gillett Cay Swain Reefs, Qld, 65-74m, 18.x.62; 2 spec., J9303, Heron Id, Qld, no coll. depth, xii.59; 1 spec., J10939, Marion Reef, Qld, 4m, 1.ix.77; 1 spec., J10940, Marion Reef, Qld, 8m, 27.viii.77; 1 spec., J15134, South Solitary Id, N.S.W., 27m, 31.i.82; 1 spec., J16602, Malabar, Lord Howe Id, 10m, 10.xii.79; 1 spec., J16856, Three Isles, Qld, 3-12m, 6.x.82; 3 spec., J19461, Heron Id, Qld, no coll. depth, 29.viii.85; 1 spec., J19577, Heron Id, Qld, no coll. depth, 23.viii.85; 1 spec., J19578, Heron Id, Qld, no coll. depth, 25.viii.85; 1 spec., J19579, Heron Id, Qld, no coll. depth, 28.viii.85.

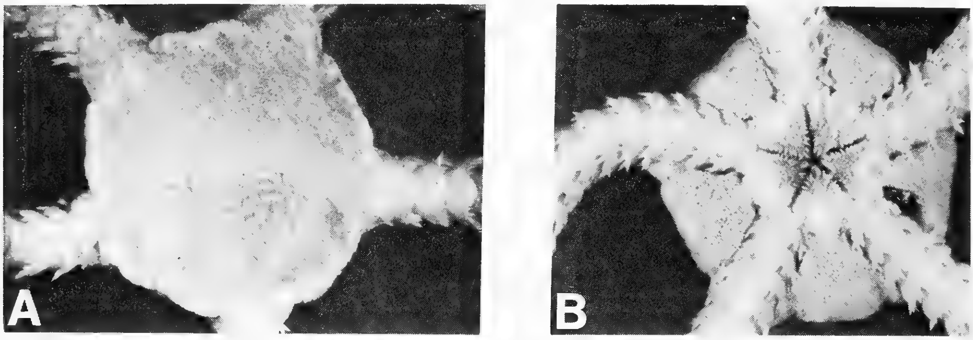

Fig. 3. **A**, **B**, *Ophiopeza spinosa*, (AM J19461), dorsal and ventral view respectively, dd = 6mm. Some disc granules were removed in **A** to show disc scaling.

Diagnosis: Disc diameter to 9mm, densely covered with small granules which are triangular in cross-section and flat-topped with a slightly depressed central area, ca 50 per mm; coarse overlapping scales underlying the granules. Each interradius with about nine marginal disc plates which are convex, prominent, and covered with larger granules than are present on the rest of the disc. Radial shields small (0.1 x d.r.), obscured by granules; only 1-2 scales separating the two plates of each pair of radial shields. Arms to 30mm, ca 5 x d.d., dorsal plates fan shaped, ca as wide as long. Nine to twelve, pointed, arm spines, less than half an arm segment long. Two tentacle scales per pore, inner one longest, outer one covering base of lowest arm spine. Oral shields longer than wide with a blunt proximal margin, supplementary plates usually present; adoral plates triangular, ca half as long as the oral shields, not contiguous. Oral plates covered with flat-topped granules. Eight to ten oral papillae; tooth papillae generally pointed.

Colour (dried): Dorsal surface cream to light grey, arms generally with dark banding; ventral surface cream, little sign of banding.

Colour (live): Kingston (1980: 145) described one live specimen as 'cream with faint brown cross-bands on the dorsal arm surface'.

Distribution: In Australia, from off Coffs Harbour, N.S.W., along the Great Barrier Reef, Qld, and in off-shore reefs of northwestern Australia. Overseas, western Indian

Ocean and the Red Sea to Indonesia, the Philippines and the western Pacific Ocean. A cryptic species often found under rocks or rubble, 3-74m.

Remarks: Both H. L. Clark (1909a) and Clark and Rowe (1971) were hesitant in recognizing *spinosa* and *dubiosa* as distinct species. De Loriol (1893b) considered *dubiosa* separate from *spinosa* because it had fewer arm spines (9 compared with 12-14) and because of its yellowish-green colour, instead of brown as in *spinosa*. We have examined 20 specimens of *spinosa* held in collections of the Australian Museum. Their disc diameters ranged from 4-9mm and their arm spine number from 9-12, overlapping the numbers supposedly characteristic of these two species. Although specimens examined by us were coloured a shade of brown, we do not consider the slight variation in colour recorded by de Loriol to be significant. In addition, our material also agrees with de Loriol's figures of *dubiosa*. Thus, we herein consider *dubiosa* to be synonymous with *spinosa*.

O. spinosa shares with *cylindrica*, *fallax*, and *arabica* the character of only a few large scales separating the two plates of each pair of radial shields. *O. spinosa* can be separated from these taxa in possessing only 1-2 scales in that position, but more readily by the distinctive shape of its disc granules.

Key to the species of *Ophiopeza*
(excluding *O. exilis*)

1 Disc completely covered with granules 2
1' Some marginal disc plates, both radial and interradial, without granules 3
2 Marginal interradial disc plates convex, conspicuous despite cover of granulation; disc granules flat-topped . . . . *O. spinosa*
2' Marginal interradial disc plates not conspicuously convex, not visible through granulation; disc granules rounded . . . . *O. cylindrica*
3 Only the middle marginal interradial disc plates are bare; radial shields covered with granules . . . . *O. fallax fallax* (Fig. 4**A, B**)
3' Some marginal disc plates, both radial and interradial, are bare; radial shields sometimes partially bare . . . . *O. fallax arabica*

Genus ***Ophiopsammus*** Lütken

Ophiopsammus Lütken, 1869: 37 (type-species *Ophiopeza yoldii*, Lütken, 1856, by monotypy).

Diagnosis: A genus of ophiodermatid with radial shields obscured by granules; marginal interradial disc scales enlarged, covered by granules, never bare; disc scales very fine, overlapping, numerous disc scales separating the two plates of each pair of radial shields; oral plates covered by granules; oral shields naked, supplementary plates absent or present; dorsal arm plates transversely rectangular (up to ca 5 x wider than long), convex to conspicuously carinate; arm spines seldom exceeding one arm segment in length, often appressed.

Other species included: *O. aequalis* (Lyman, 1880), *O. anchista* (H. L. Clark, 1911), *O. angusta* sp. nov., *O. assimilis* (Bell, 1888), *O. maculata* (Verrill, 1869).

Remarks: We support A. M. Clark's (1968) resurrection of *Ophiopsammus*, but not solely on the basis of its carinate dorsal arm plate shape. In addition, our studies have shown the importance of disc scaling in recognizing *Ophiopsammus*. This genus differs from

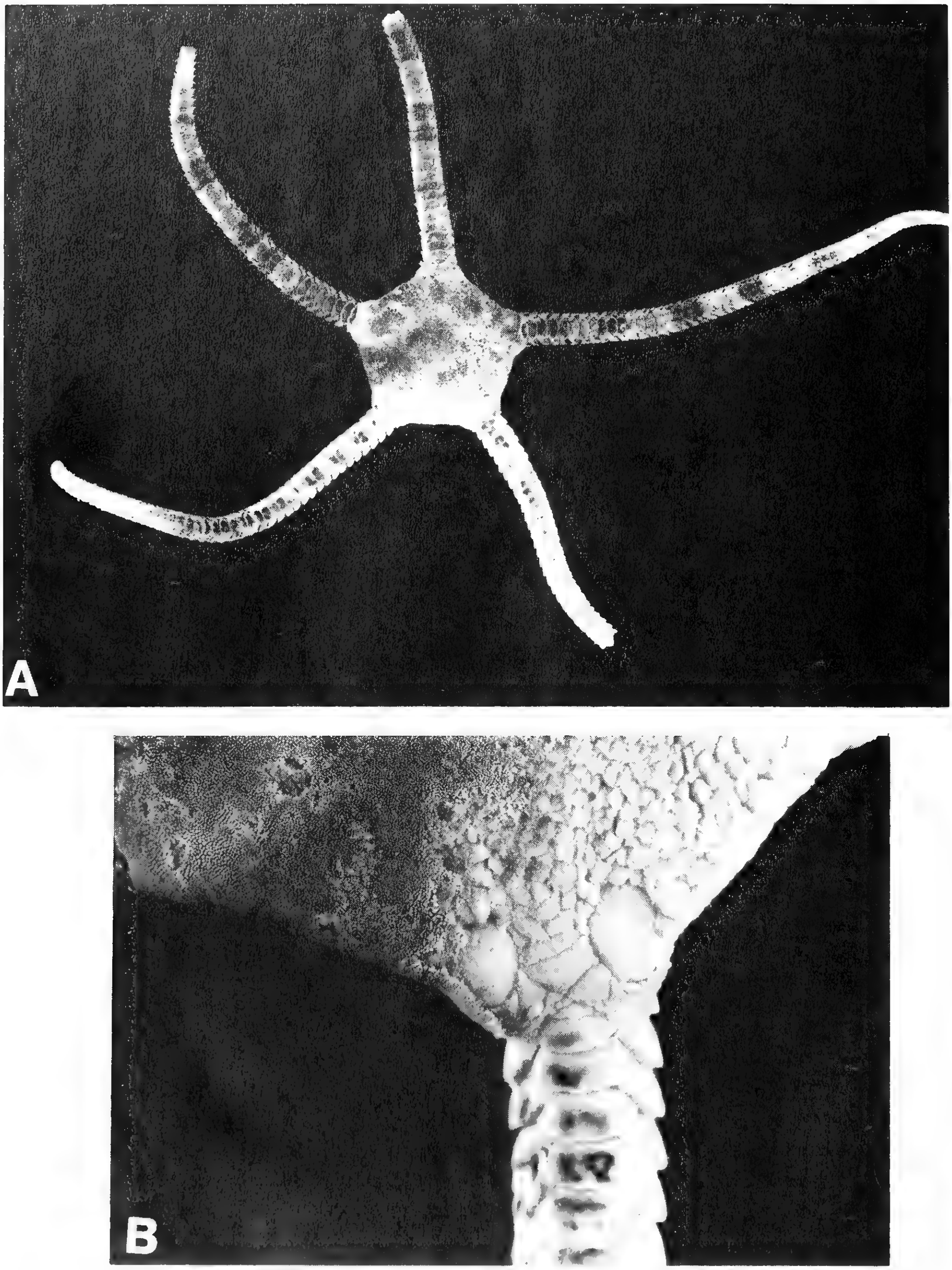

Fig. 4. **A. B.** *Ophiopeza fallax fallax*, (BM (NH) 1965.6.1.507), dorsal view, dd = 14mm. Some disc granules were removed to show disc scaling.

Ophiopeza in having relatively finer disc scaling, and numerous small scales separating the two plates of each pair of radial shields. In addition, the dorsal arm plates are wide and transversely rectangular shaped. The species we include in *Ophiopsammus* also attain a greater size (d.d. to ca 41mm, arm length to ca 180mm) than those of *Ophiopeza* (d.d to ca 11mm, arm length to ca 40mm).

Ophiopsammus yoldii Lütken, 1856

Fig. 5**A,B**

Ophiopeza yoldii Lütken, 1856: 9. Lyman, 1874: 221.
Ophiopsammus yoldii. Lütken, 1869: 37. A. M. Clark, 1968: 317, fig. 9a, b. Clark and Rowe, 1971: 90, 127, pl. 21, figs 7, 8. Gibbs *et al.*, 1976: 130. Kingston, 1980: 145.
Ophiopeza conjungens. Bell, 1884: 137. Döderlein, 1896: 281, pl. 15, fig. 1.
Pectinura yoldii. H. L. Clark, 1909a: 119; 1921: 141; 1938: 344. Koehler, 1922: 338, 1930: 270.

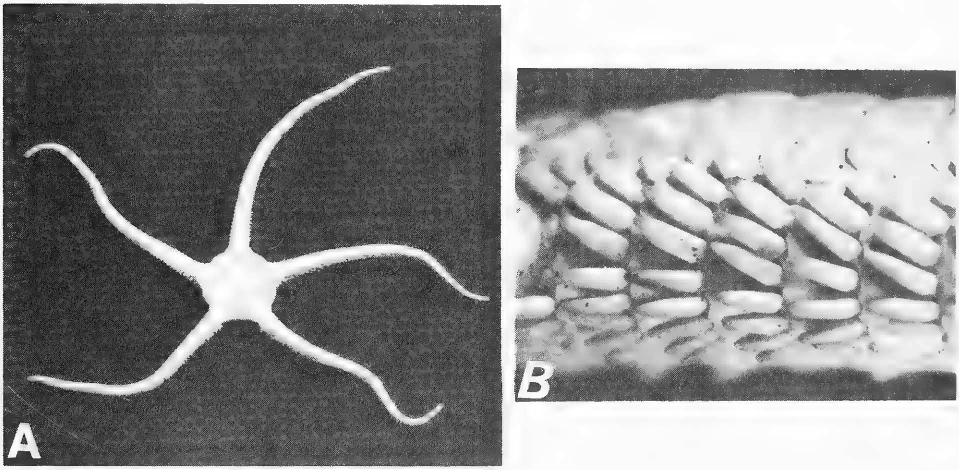

Fig. 5. Ophiopsammus yoldii, (AM J5374), dd = 22mm. **A**, dorsal view, some disc granules were removed; **B**, arm spines (proximal) and a portion of dorsal arm plate (top of photo).

Material Examined: (All specimens examined are held in the AM) 3 spec., G4208, Mapoon, Gulf of Carpentaria, Qld, no coll. depth or date; 1 spec., G4983, Port Curtis, Qld, no coll. depth or date; 1 spec., G11420, Port Denison, Qld, no coll. depth or date; 4 spec., J2413-16, Port Curtis, Qld, no coll. depth or date; 2 spec., J5307, Albany Passage, Qld, 17-22m, ix.28; 2 spec., J5374, off Gatcombe Head, Port Curtis, Qld, 17-22m, vii.29; 3 spec., J5375, off Gatcombe Head, Port Curtis, Qld, 17-22m, vii.29; 1 spec., J5487, Port Curtis, Qld, no coll. depth or date; 1 spec., J5924, Kennedy Sound, nr Whitsunday Passage, Qld, 15m, no coll. date; 1 spec., J8889, off Gillett Cay, Swain Reefs, Qld, 65-74m, 19.x.62; 1 spec., J8890, off Gillett Cay, Swain Reefs, Qld, 65-74m, 18.x.62; 1 spec., J9306, Gulf of Carpentaria, Qld, <26m, ix.64; 1 spec., J11227, SE corner of Gulf of Carpentaria, Qld, no coll. depth or date; 1 spec., J12208, nr Turtle Head Id, Cape York, Qld, no coll. depth, 15.ii.79; 12 spec., J12228, Cape York, Qld, no coll. depth, 15.ii.79; 1 spec., J18001, Abbot Pt, Bowen Qld, 15-17m, 11.vi.83; 5 spec., J18002, Abbot Pt, Bowen, Qld, 6-11m, 11.vi.83; 4 spec., J18009, Abbot Pt, Bowen, Qld, 11-12m, 11.vi.83; 2 spec., J18010, Abbot Pt, Bowen, Qld, 15-17m, 11.vi.83; 1 spec., J18013, Abbot Pt, Bowen, Qld, 16m, 12.vi.83; 2 spec., J18016, Abbot Pt, Bowen, Qld, 10-16m, 12.vi.83; 2 spec., J18017, Abbot Pt, Bowen, Qld, 5-19m, 10.vi.83; 1 spec., J18018, Abbot Pt, Bowen, Qld, 5-19m, 10.vi.83; 2 spec., J18048, Abbot Pt, Bowen, Qld, 5-6m, 19.vi.82; 2 spec., J18049, Abbot Pt, Bowen, Qld, 14-15m, 11.vi.83; 1 spec., J18345, 74 n.m. NNE

Pt Hedland, W.A., 80m, 30.x.83; 1 spec., J18370, 50 n.m. NNE Pt Hedland, W.A., 38-40m, 25.x.83; 1 spec., J18400, 52 n.m. NNE Pt Hedland, W.A., 36-37m, 24.x.83; 1 spec., J18409, 52 n.m. NNE Pt Hedland, W.A., 36-37m, 24.x.83; 1 spec., J18478, 80 n.m. NNE Pt Hedland, W.A., 82m, 23.x.83; 1 spec., J18497, 80 n.m. NNE Pt Hedland, W.A., 83m, 23.x.83.

Diagnosis: Disc diameter to 22mm, densely covered with rounded granules, 14-23 per mm; fine, overlapping scales underlying the granules. Each interradius with about 9 marginal disc plates, obscured by granule cover, middle plate the largest. Radial shields 0.3 x d.r., obscured by granules, the two plates of each pair of radial shields separated by numerous scales. Arms to 75mm, 1.8-3.1. x d.d.; dorsal arm plates mainly transversely rectangular in shape (2-5 x wider than long) but becoming fan shaped near the arm tip, carinate, even in small specimens, usually entire but occasionally fragmented; ventral arm plates ca as long as wide in small specimens (d.d. $\lesssim$ 10mm), becoming wider than long (up to 2 times) in larger specimens, distalmost margin slightly irregular. Five to ten stout arm spines, middle ones longest (sometimes slightly exceeding an arm segment in length) and in large specimens (d.d. $\lesssim$ 20mm) also wider than the remaining spines. Two tentacle scales per pore, inner one larger, ca half the length of lowest arm spine and distinctly curved, outer one covering base of lowest arm spine. Supplementary oral shields generally absent, rudimentary when present. Oral shields pentagonal in small specimens, becoming heart-shaped with growth, flat, ca as wide as long; adoral plates small, triangular, not contiguous. Oral plates covered with granules. Ten to twelve oral papillae; tooth papillae pointed.

Colour (dried): Dorsal surface light grey or brown to a darker reddish brown, ventral surface generally a lighter shade of the dorsal surface colour. Some specimens have mottled cream and grey discs with grey banding on cream coloured arms, while others have a large, light stellate pattern in the disc centre contrasting with a darker background.

Distribution: In Australia, along the Great Barrier Reef and in the Gulf of Carpentaria, Qld, and off Pt Hedland, W.A.; 5-83m. Overseas, the species has been recorded from the Bay of Bengal to the Philippines Ids, to 215m.

Remarks: Housed in the Australian Museum is a collection of approximately 60 specimens of *Ophiopsammus yoldii* and 40 specimens of *Ophiopsammus assimilis.* Examination of dorsal disc scaling in these specimens has shown the two species to be very similar. In fact, the very distinctive arm spine arrangement of *yoldii* is the only character we can find to separate it from *assimilis.* In *yoldii,* the middle arm spines are longest (ca one arm segment long), whereas in *assimilis* all arm spines are of approximately equal length (ca ½-⅔ of an arm segment long). Characters separating *yoldii* from its congeners are given in the key.

Ophiopsammus aequalis (Lyman, 1880)
Fig. 6**A-C**

Ophiopeza aequalis Lyman, 1880: 9, pl. 2, figs 23-25; 1882: 12, pl. 27, figs 7-9. Koehler, 1904: 10; 1922: 337, pl. 77, figs 16, 17. A. M. Clark, 1968: 313.
Pectinura aequalis. H. L. Clark, 1909a: 118; 1915: 303.

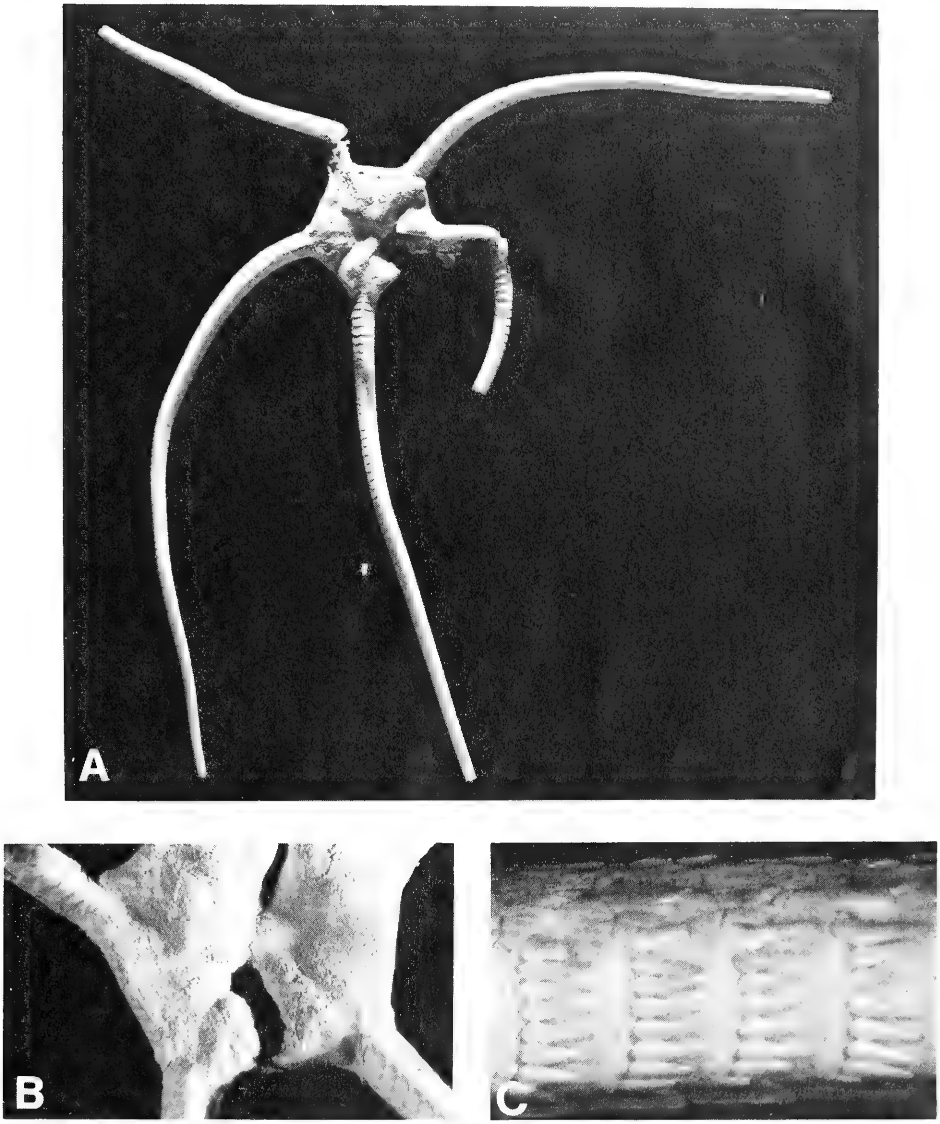

Fig. 6. Ophiopsammus aequalis, (AM J13960; 2 specimens, i and ii). **A**, dorsal view, specimen i, dd = 23mm; **B**, dorsal view, specimen ii, dd = 26mm; **C**, arm spines (proximal) and ventral arm plates (bottom of photo), specimen i. Some disc granules were removed in **A** and **B**.

Material examined: 3 spec., AM J13960, Timor Sea, northern Australia (09° 48′S, 129° 23′E), 270-272m, 25.vi.79.

Diagnosis: Disc diameter to 23mm, densely covered with small, round granules, ca 15 per mm; exceedingly fine overlapping scales underlying the granules. Each interradius with eleven marginal interradial disc plates, slightly convex, middle one largest, all covered by granules. Radial shields 0.15-0.2 x d.r., obscured by granules; numerous scales separating the two plates of each pair of radial shields. Arms to ca 140mm (tips broken), ca 5-6 x d.d.; dorsal arm plates transversely rectangular (2-3 x wider than long) and strongly carinate. Nine to ten pointed arm spines, ½-⅔ of an arm segment long, lowest spine marginally longer and wider than the remaining spines. Two tentacle scales per pore, inner one longer, outer one covering base of lowest arm spine. Oral shields slightly wider than long, proximal margin blunt, distal margin broadly convex, some oral shields with a rudimentary supplementary plate; adoral plates small, ca 0.2-0.3 x oral shields long, not contiguous. Oral plates covered by numerous granules. Eight to nine oral papillae, penultimate very long (up to 3 x longer than the other papillae); tooth papillae blunt.

Colour (dried): Cream to light grey both dorsally and ventrally. Koehler (1922: 337) records one preserved specimen with a pink dorsal disc surface and arms with light pink and dark red annulations.

Distribution: Lyman's types came from northeast of New Guinea and the Kei Islands. Additional specimens were collected by the 'Siboga' northeast of northern Borneo. The three specimens examined by us from the Timor Sea are the first records of this species from Australia. This is a deep-water ophiodermatid species previously collected from 209-274m.

Remarks: Long delicate arms are common to both *O. aequalis* and *O. angusta* sp. nov., in contrast to the relatively shorter, stouter arms of *O. assimilis* and *O. yoldii*. However, *aequalis* is easily separated from *angusta* on differences in arm spine arrangement and from the New Zealand species *O. maculata* on the shape of dorsal arm plates. Characters separating *aequalis* from its congeners are illustrated in the key.

Ophiopsammus assimilis (Bell, 1888)

Fig. 7**A-C**

Pectinura assimilis. Bell, 1888: 282, pl. 16, fig. 5. H. L. Clark, 1909a: 118; 1946: 257. A. M. Clark, 1966: 327. ?Baker, 1982: 436.

?*Ophiopeza cylindrica.* Farquhar, 1898a: 190; pl. 14, figs 4, 5 [non *cylindrica* Hutton, 1872.]

Pectinura dyscrita. H. L. Clark 1909b: 534, pl. 49, figs 5-7. Dartnall, 1980: 42, 71. H. L. Clark, 1946: 256.

?*Pectinura cylindrica.* Mortensen, 1924: 172, fig. 35(1-2) [non *cylindrica* Hutton, 1872.]

Pectinura nigra. H. L. Clark, 1938: 344. H. L. Clark, 1946: 256.

Ophiopeza dyscrita. A. M. Clark, 1968: 313. Baker, 1982: 436.

Ophiopeza nigra. A. M. Clark, 1968: 313.

Material examined: Holotype of *assimilis* BM(NH) 86.6.9.23, Port Jackson, N.S.W., no coll. depth or date; **holotype** of *nigra* MCZ 5257, Koombana Bay, Bunbury, W.A., 9-15m, 26.x.1929; 1 **lectotype** of *dyscrita* AM J849, off Wata Mooli, N.S.W., 129-144m, no coll. date; 2 spec., AM E5941, 30 mls S. of Mt Cann, Gippsland, Vic., 129-185m, 19.x.14; 1 spec., AM J11637, Long Reef, Collaroy, N.S.W., 40m, 14.iv.72; 1 spec., AM G11418, Port Jackson, N.S.W., no coll. depth or date; 4 spec., AM J15991, (32° 52.51′S, 152° 34.35′E), 151m, 6.xii.78; 1 spec., AM G11440, Port Jackson, N.S.W., no coll. depth or date; 1 spec., AM J10008, E of Cronulla, N.S.W. (34° 09′S, 151° 16′E), 127-132m, 17.iv.75; 3 spec., AM J14978, Julian Rocks, Byron Bay, N.S.W., 12m, 4.ii.82; 1 spec., AM J18557, nr Mistaken Id, Albany, W.A. (35° 04′S, 117° 56′E), 2m, 13.x.83; 1 spec.,

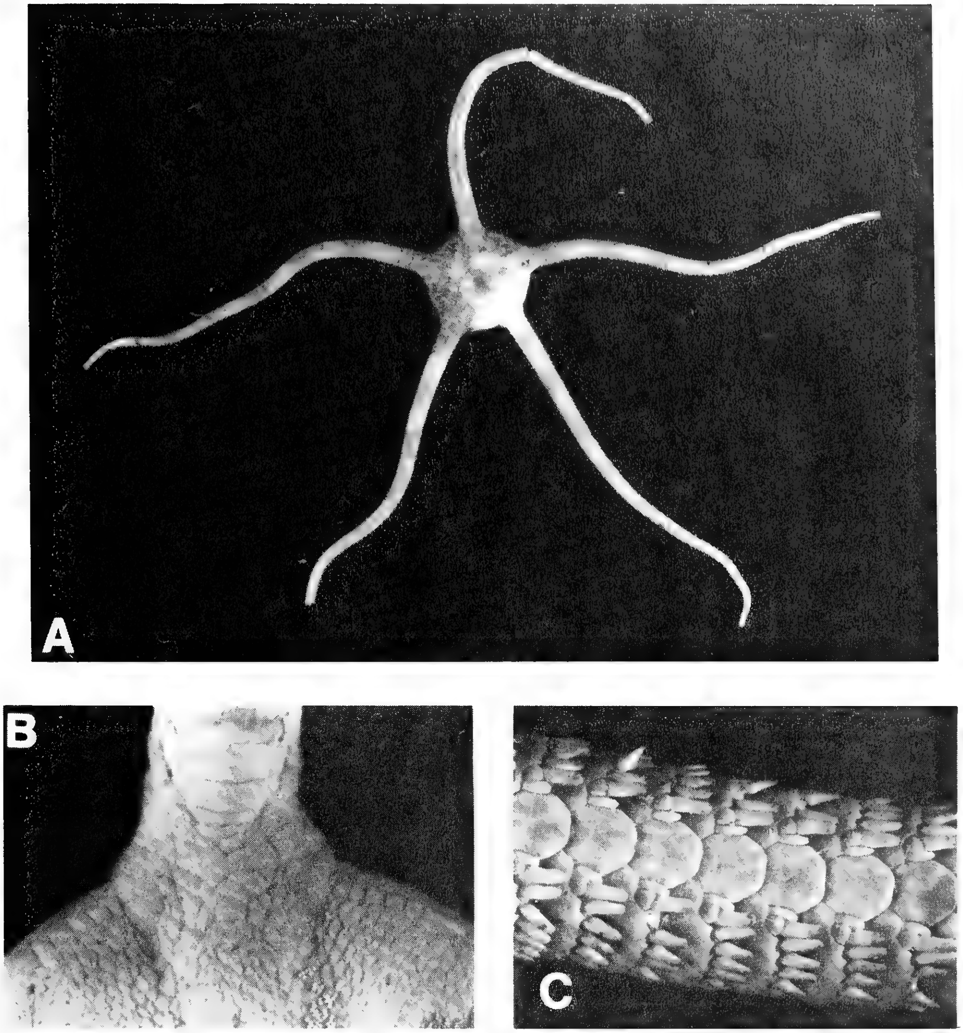

Fig. 7. Ophiopsammus assimilis, holotype (BM (NH) 86.6.9.23), dd = 24mm. **A** and **B**, dorsal view, some disc granules were removed: **C**, ventral arm plates and arm spines (proximal).

AM J14979, Julian Rocks, Byron Bay, N.S.W., 9-15m, 3.ii.82; 1 spec., AM E4717, Gabo Id, Vic., 368m, no coll. date; 1 spec., AM G7115, Port Hacking, N.S.W., 55-74m, 1961; 1 spec., AM J12564, NE side Kangaroo Id, S.A., 5m, 9.iii.78; 1 spec., AM G11419, Port Jackson, N.S.W., no coll. depth or date; 1 spec., AM J17621, Triggs Id, Perth, W.A., 6m, 22.v.83; 3 spec., AM E5212, E of Babel Id, Tas., 129m, 1914; 4 spec., AM J11086, 40mls ENE of Sydney, N.S.W., 184-232m, 18.vi.59; 1 spec., AM G11027, Port Jackson, N.S.W., no coll. depth or date; 2 spec., AM J13975, Montague Id, N.S.W., 28-31m, 16.iii.81; 1 spec., AM J14159, Ulladulla, N.S.W., 25m, 27.iii.81; 1 spec., AM J13991, Montague Id, N.S.W., 31m, 16.iii.81; 1 spec., AM J14015, Burrewarra Pt, N.S.W. (35° 50′S, 150° 14′E), 28m, 15.iii.81; 2 spec., AM J14162, Jervis Bay, N.S.W., 25-28m, 21.iii.81; 3 spec., AM G2032, Wellington, N.Z., no coll. depth, xi.1896; 2 spec., AM G11423, Port

Jackson, N.S.W., no coll. depth or date; 1 spec. AM J4306, Shell Harbour, N.S.W., no coll. depth, 21.iii.77.

Diagnosis: Disc diameter to 28mm, densely covered with rounded granules, 8-15 per mm; very fine, overlapping scales underlying the granules. Each interradius with 8-14 marginal plates, all concealed by granulation. Radial shields 0.2 x d.r., obscured by granules, up to seven overlapping scales separating the two plates of each pair of radial shields. Arms to 100mm, 2.3-4.7 x d.d.; dorsal arm plates convex to carinate, transversely rectangular (1.7-2.7 times wider than long); ventral arm plates as wide as long. Arm spines stout, tapering, slightly swollen at the base, ca half an arm segment long, 4-11 spines per lateral plate. Two tentacle scales per pore, inner one the longer. Oral shields usually without a supplementary oral plate, poorly developed if present; adoral plates small, not contiguous. Oral plates covered with granules. Seven to eight blunt oral papillae on each half jaw; penultimate conspicuously wider than the others; tooth papillae stout, blunt.

Colour (dried): Variable, cream to reddish brown to grey; arms sometimes with faint banding.

Colour (live): Some specimens may have a bright red disc and arms with alternating bands of red and grey while others have a red/cream mottled disc.

Distribution: A few individuals have been collected near Perth and Albany, W.A. and one from Kangaroo Id, S.A. This species has been more commonly found in Tas. and from off Gabo Island, Vic., to Byron Bay, N.S.W., on the Australian coast. It also occurs in New Zealand, at least along the northern coasts from Three Kings Id to Cook Strait. This species is quick moving and is found under rocks (pers. obs. L.V.), at least in shallower depths; depth range 2-368m.

Remarks: The original description of *Ophiopeza assimilis* Bell, 1888, is based on one specimen with a disc diameter of ca 100mm and arm length of 24mm. We have examined a specimen from the British Museum (86.6.9.23) labelled as a type of *assimilis* with a disc diameter of 24mm and arm length of ca 90mm. We consider this specimen the holotype of *assimilis* since it fits Bell's description and has the same locality data. Only its disc diameter and arm length measurements disagree with the original description and these have obviously only been reversed.

As discussed previously (p. 272), figures given for *Ophiopeza cylindrica* by both Farquhar (1898a) and Mortensen (1924) probably represent *assimilis*. This view is supported by material in the Australian Museum collections from New Zealand (AM G2032). Positive identification of the material figured by them would have required removal of some dorsal disc granules in order to reveal the pattern of disc scaling between the plates of each pair of radial shields, but this material was not available.

In a revision of the genus *Pectinura*, H. L. Clark (1909a) separated *arenosa* (now regarded as a synonym of *Ophiopeza cylindrica*) and *assimilis* on the size of their dorsal arm plates and on the presence or absence of supplementary oral shields. Specimens described herein as *cylindrica* have supplementary oral plates associated with most oral shields (Table 1). These plates are generally absent in *assimilis*, although some individuals (AM; G7115, J14978 (2), E5941) have rudimentary supplementary oral plates. The disc granules of *cylindrica* and *assimilis* have never featured in descriptions of these species and consequently two characters which readily separate them have been overlooked: namely the arrangement of scales separating the two plates of each pair of radial shields, and the type of disc scaling.

Shortly after his revision of *Pectinura*, H. L. Clark (1909b) described a new species, *dyscrita*, from two specimens collected off central N.S.W. (**lectotype** AM J5849; **paralectotype** MCZ 590, designated herein). He noted they were most similar to *assimilis* but differed in having fewer (6-8) arm spines. Another species, *nigra*, was described by H. L. Clark (1938) from one specimen collected near Bunbury, Western Australia. H. L. Clark (1946) separated *nigra* and *dyscrita* on arm spine number and by the black coloration of *nigra*. We have examined the holotype of *nigra* (d.d. 7mm) and the lectotype of *dyscrita* (d.d. 10mm) and confirm that their disc scaling is the same as that of *assimilis*. Furthermore, differences in their arm spine number and coloration are within the range of variation found in *assimilis*. However, as more material is collected, it may be shown that the darker coloration which Clark attributed to *nigra* is more common in specimens from South Australia and westwards. H. L. Clark (1909; 1946) also distinguished *dyscrita* from other species of *Ophiopeza* by its large lowest arm spine. Our examination of the lectotype material of *dyscrita* has shown its lowest arm spine is only marginally longer, if any, than the other arm spines. Thus, we now regard both *dyscrita* and *nigra* as synonyms of *assimilis*.

Interestingly, an enlarged lowest arm spine is one character readily separating adults of *Ophiopsammus angusta* sp. nov. (p. 285) and *assimilis*. In addition, the lowest arm spine of *angusta* is broader than the other spines and its arm spines have straight marginal edges in contrast to the tapering ones of *assimilis*. *O. assimilis* is most readily separated from its other congeners on arm spine arrangement and dorsal arm plate shape as shown in the key. Large New Zealand specimens, however, occasionally have fragmented dorsal arm plates (A. N. Baker, pers. comm.).

Ophiopsammus angusta sp. nov.

Fig. 8**A-C**

Material Examined: Holotype, AM E4693, E of Flinders Id, Bass Strait, Tas., 148-553m; no coll. date; 1 **paratype**, AM E5025, E of Maria Id, Tas., 144m, no coll. date; 1 **paratype**, Am E5376, NE of Cape Pillar, Tas., 148m, 1914; 1 **paratype** AM E5946, Bay of Fires, Tas., 102m, 7.xi.14; 1 **paratype**, MV F52197, S of Cape Nelson, Vic., 406m, 10.iii.77; 1 spec., AM E5116, E of Maria Id, Tas., 236m, no coll. date; 10 spec., MV F52196, Bass Strait, 38° 52.6′S, 148° 25.2′E, 140m, 15.xi.81; 1 spec., MV F52194, S of Bemm River, Vic., 38° 15.1′S, 149° 00′E, 223m, 22.xi.73; 1 spec., MV F52195, W of Cape Nelson, Vic., 165-201m, 6.vi.69.

Diagnosis: Disc diameter to 21mm; rounded granules, 7-14 per mm; fine overlapping scales on the dorsal and ventral surfaces; 9-14 marginal disc plates per interradius, middle one largest. Radial shields ca 0.1-0.2 x d.r., about twice as long as wide, the two plates of each pair separated by ca 8 disc scales, radial shields obscured by disc granulation. Arms to 116mm, 5.5-7.9 x d.d., dorsal arm plates transversely rectangular (ca 1.5 x wider than long), slightly carinate, distal margins slightly convex; ventral arm plates roughly hexagonal with rounded corners (ca as wide as long), distal margin convex; 8-10 arm spines, ca half the length of an arm segment; lowest arm spine the longest, conspicuously wider than the other arm spines. Lateral margins of arm spines generally parallel, tapering on the distal ⅓ of their length. Two tentacle scales per pore, inner one the longer. Oral shields roughly triangular with round edges, supplementary plates usually absent; adoral plates longer than wide, not contiguous. Oral plates covered with

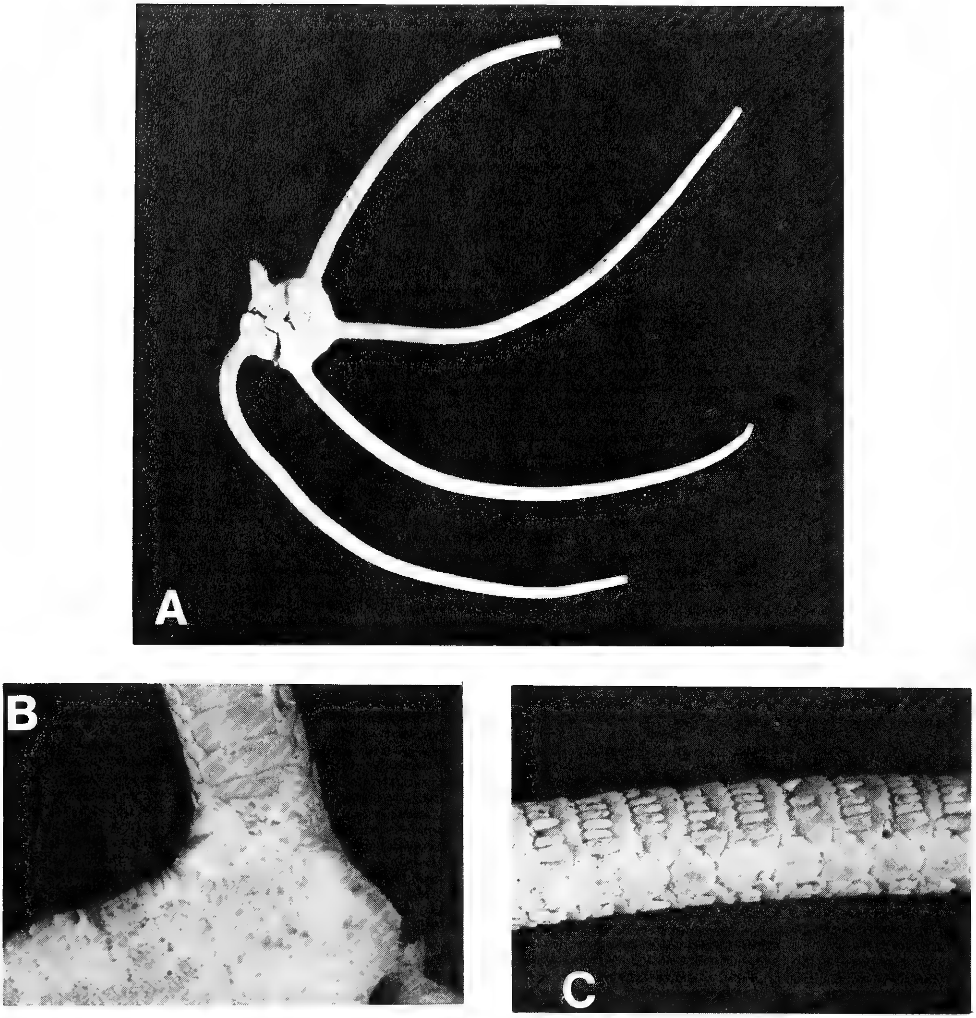

Fig. 8. **A-C**, *Ophiopsammus angusta* sp. nov., holotype (AM E4693), dd = 17.5mm. **A** and **B**, dorsal view, some disc granules were removed; **C**, ventral arm plates and arm spines (proximal).

granules. Six to seven oral papillae on each half jaw, penultimate at least 2 x wider than the remainder; tooth papillae stout, blunt.

Description of Holotype: Disc diameter 17.5mm; covered with granules both dorsally and in the ventral interradial areas, 7-9 granules/mm. Fine, overlapping disc scales occur both on the dorsal and ventral surfaces. Each interradius with thirteen marginal disc plates, middle one the largest. Radial shields 0.2 x d.r. (ca twice as long as wide), the two plates of each pair separated by ca 8 disc scales. Disc scales, marginal plates and radial shields obscured by disc granulation.

Arms broken, to ca 100mm, 5.7 x d.d., very finely tapered, slightly carinate dorsally. Dorsal arm plates transversely rectangular with a slightly convex distal margin (ca 1.5-

1.7 x wider than long), distally becoming more fan shaped with a convex distal margin. First ventral arm plate transverse diamond shaped (ca 2 x wider than long), distal margin convex. Succeeding arm plates roughly hexagonal with rounded corners (ca as wide as long), distal margin convex; distal plates becoming slightly longer than wide. First lateral arm plate with 2 arm spines, 2nd and 3rd-4, 4th and 5th-6, 6th-8, thereafter 9, decreasing at the distal end of the arm to 6 spines. Lowest arm spine longest (¾-1 arm segment long) and widest (ca 1.25 x wider than the other spines). Remaining arm spines ca ½ an arm segment long, proximal ⅔ of each spine with parallel lateral margins, becoming slightly tapered distally with a blunt tip; adjacent spines contiguous or almost contiguous. Two tentacle scales per pore; inner one the longer, tapering distally; outer one covering proximal portion of lowest arm spine (ca as broad as long), with a blunt distal margin.

Oral shields roughly triangular with very rounded edges (ca as long as broad), one shield with a rudimentary, distal, supplementary plate; adoral plates triangular (longer than wide); not contiguous. Oral plates densely covered with granules about equal in size to the disc granules. Six to seven oral papillae on each half jaw, penultimate ca 3 x wider than the other papillae. Tooth papillae stout with pointed or blunt tips.

Paratypes: Disc diameters ranged from 11-21mm and maximum arm lengths from ca 60-116mm. Except for overall size and arm spine number, the paratypes do not differ from the holotype. Arm spine number ranged from 8-10 per plate, with the smallest specimen (d.d. 11mm) having the fewest arm spines and the largest (d.d. 21mm) the most.

Colour (dried): Holotype, creamy white; other material, creamy white to light grey; one specimen (NMV F52195) is a uniform light purple.

Distribution: Endemic to southeastern Australia; off Tas. and Vic.; 102-201m.

Etymology: The species is named from the Latin *angustia* for the straight sided arm spines.

Remarks: *O. angusta* appears most closely related to *assimilis*. Characters separating them are: the R/d.d. ratio; shape of the lowest arm spine; and shape of the other arm spines. In *angusta*, R/d.d. is 5.5-7.9 for individuals with a d.d. >9mm while in similar-sized specimens of *assimilis*, this ratio is 2.3-4.7. Consequently, the arms of *angusta* appear delicate while those of *assimilis* seem stout and robust. The lowest arm spine of *angusta* is noticeably longer, wider, and more robust in appearance than other arm spines whereas in *assimilis*, this spine is only slightly, if any, longer and wider than the other spines. In larger specimens of *angusta* (d.d. >9mm), lateral margins of arm spines are nearly parallel, except near the tip where they begin to taper. In contrast, specimens of *assimilis* (d.d. > 9mm) have more tapered arm spines. In addition, lateral margins of arm spines in *angusta* are almost contiguous whereas in *assimilis* they are separated.

We have been unable to satisfactorily separate small specimens (d.d. < 9mm) of *angusta* and *assimilis* as their R/d.d. ratio is very similar (ca 3.0-4.0) and their arm spines appear similar. Relative size of the lowest arm spine is most useful when separating small specimens. A collection of 9 small specimens (d.d. 6-8mm) of *Ophiopsammus* from Bass Strait (MV F52196) are probably *angusta* because of their long and wide innermost arm spines.

O. angusta shares with *aequalis* and *anchista* a high R/d.d. ratio and thus delicate-appearing arms, although the very carinate dorsal arm plates in *aequalis* readily separate

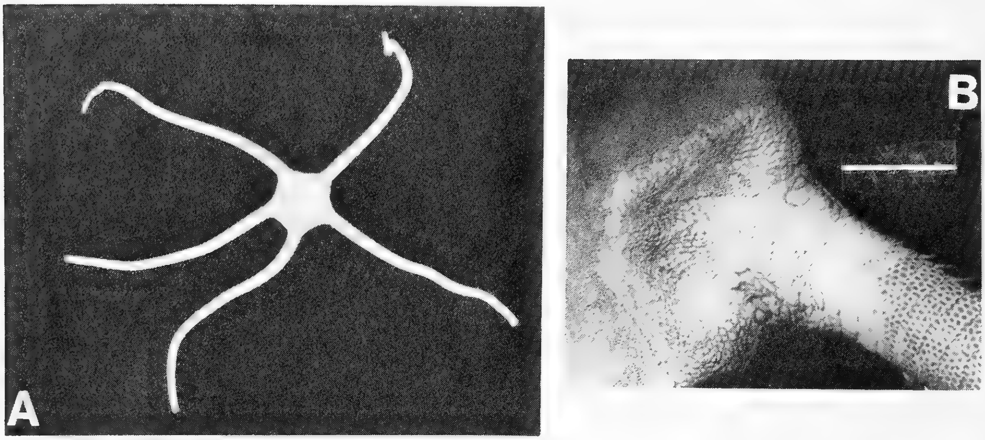

Fig. 9. **A**, *Ophiopsammus anchista*, holotype (USNM 25645), dorsal view, dd = 13mm. **B**, *Ophiopsammus maculata*, (AM J10208), dorsal view, scale line = 10mm.

it from these two other taxa. Differences between *angusta* and its other congeners are demonstrated in the key.

Notes on *Ophiopsammus anchista* (H. L. Clark, 1911)

During this study, we examined a holotype (USNM 25645, Fig. 9**A**) and two paratypes (USNM 26214) of *anchista* H. L. Clark, 1911 from Japan. The species is referable to *Ophiopsammus*. However, the smallest paratype (d.d. ≲ 4mm) is misidentified, being identified by us as a species of the genus *Cryptopelta* H. L. Clark, 1909a.

O. anchista is most readily separated from its other congeners on the shape of its arms, dorsal arm plates, and arm spines, as shown in the key.

Key to the species of *Ophiopsammus*

1 Dorsal arm plates often very fragmented, usually spotted. . . . . . *O. maculata* (Fig. 9)
1' Dorsal arm plates entire, except for *O. yoldii* which may have a few fragmented plates; not spotted 2
2 Arms long, delicate appearance (R/d.d. ratio 5-8 in adults) 3
2' Arms relatively short, stout appearance (R/d.d. ratio 1.8-4.7) 5
3 Dorsal arm plates strongly carinate . . . . *O. aequalis*
3' Dorsal arm plates round to only slightly carinate 4
4 Lowest arm spines distinctly longer and wider than adjacent arm spines; lateral margins of arm spines parallel on proximal ⅔ of spine; arm segment no. 10 with ca 9 arm spines . . . . *O. angusta*
4' Lowest arm spines ca the same length as adjacent arm spines; arm spines tapered, arm segment no. 10 with ca 6 arm spines . . . . *O. anchista*
5 Arm spines on each segment of ca same length, about ½ an arm segment long . . *O. assimilis*
5' Middle arm spines the longest, to about one arm segment long . . . . *O. yoldii*

ACKNOWLEDGEMENTS

Miss A. M. Clark, British Museum (Natural History), London, U.K., Prof. R., Woollacott, Museum of Comparative Zoology, Harvard, Mass., U.S.A., Dr A. N.

Baker, National Museum of N.Z., Wellington, N.Z., Dr Suzanne Boyd, National Museum, Melbourne, Victoria, Australia, are thanked for the loan of type specimens.

Dr F. W. E. Rowe wishes to acknowledge support for this project from both the Australian Research Grants Scheme (ARGS D18015325) and Marine Sciences and Technologies Grant Scheme (MST 84/2092). We wish to thank Ms Kate Lowe, Photographic Department, Australian Museum, and Mr Alan Howard, Northern Territory Museum, for photographing specimens illustrated in this work and Mrs L. Watt, Northern Territory Museum, for typing the manuscript. Finally, we wish to thank Ms A. Hoggett, N.T. Museum, and Dr A. N. Baker, National Museum of N.Z., for reading and commenting on the manuscript.

References

BAKER, A. N., 1982. — Brittle-stars (Class Ophiuroidea). *In:* S. A. SHEPHERD and I. M. THOMAS, (eds), *Marine Invertebrates of South Australia*. Part I: 418-437. Adelaide: South Australian Govt Printer.

BELL, J. F., 1884. — Echinodermata. *In* R. W. COPPINGER: *Report on the zoological collections made in the Indo-Pacific Ocean during the voyage of H.M.S. 'Alert', 1881-2*: 117-177, 509-512. London: British Museum (Natural History).

——, 1888. — Descriptions of four new species of ophiuroids. *Proc. zool. Soc. Lond.*: 281-284.

CLARK, A. M., 1966. — Port Phillip Survey 1957-1963, Echinodermata. *Mem. Nat. Mus. Vict.* 27: 289-384.

——, 1968. — Notes on some tropical Indo-Pacific Ophiotrichids and Ophiodermatids (Ophiuroidea). *Bull. Brit. Mus. (nat. Hist.), Zool.* 16(7): 277-322.

——, and ROWE, F. W. E., 1971. — *Monograph of shallow-water Indo—west Pacific echinoderms*. London: British Museum (Natural History).

CLARK, H. L., 1909a. — Notes on some Australian and Indo-Pacific echinoderms. *Bull. Mus. comp. Zool. Harv.* 52(7): 107-137.

——, 1909b. — 'Thetis' echinoderms. *Mem. Aust. Mus.* 4: 519-564.

——, 1911. — North Pacific ophiurans in the collection of the United States National Museum. *Bull. U.S. natn. mus.* 75: v-xvi, 1-302.

——, 1915. — Catalogue of recent ophiurans: Based on the collection of the Museum of Comparative Zoology. *Mem. Mus. comp. Zool. Harv.* 25(4): 165-376.

——, 1921. — The echinoderm fauna of Torres Strait: its composition and its origin. *Pap. Dep. mar. Biol. Carnegie Instn Wash.* no. 10: 1-223.

——, 1938. — Echinoderms from Australia. *Mem. Mus. comp. Zool. Harv.* 55.

——, 1946. — *The echinoderm fauna of Australia.* Washington, D.C.: Publs Carnegie Instn no. 566: 1-567.

DARTNALL, A., 1980. — *Tasmanian Echinoderms.* Univ. of Tasmania fauna handbook no. 3: 1-82.

DÖDERLEIN, L., 1896. — Bericht über von Herrn Prof. Semon bei Amboina und Thursday Island gesammtten Ophiuroidea. *Denkschr. med.-naturw. Ges. Jena* 8: 279-300.

FARQUHAR, H., 1895. — Notes on some New Zealand echinoderms. *Trans Proc. N.Z. Inst.* 1894, 27: 194-208.

——, 1898a. — A contribution to the history of N.Z. echinoderms. *J. Linn. Soc. Zool.* 26: 186-196.

——, 1898b. — On the echinoderm fauna of New Zealand. *Proc. Linn. Soc. N.S.W.* 3: 300-327.

FORBES, E., 1842. On the radiata of the eastern Mediterranean. Part I. *Trans Linn. Soc. Lond.* 19(1): 143-153.

GIBBS, P. E., CLARK, A. M., and CLARK, C. M., 1976. — Echinoderms from the northern region of the Great Barrier Reef, Australia. *Bull. Brit. Mus. (Nat. Hist.), Zool.* 30(4): 103-144.

HUTTON, F. W., 1872a. — Catalogue of the Echinodermata of New Zealand. *Col. Mus. and geol. Surv. Dept, N.Z.*: vi + 17.

——, 1872b. — Descriptions of some new star-fishes from New Zealand. *Proc. zool. Soc. Lond.*: 810-812.

KINGSTON, S. C., 1980. — The Swain Reefs Expedition: Ophiuroidea. *Rec. Aust. Mus.* 33(3): 123-147.

KOEHLER, R., 1904. — Ophiures de mer profonde. *'Siboga' Exped.* 45: 1-176.

——, 1905. — Ophiures littorales. *'Siboga' Exped.* 45b: 1-142.

——, 1922. — Ophiurans of the Philippine Seas. *Bull. U.S. natn. Mus.* 100(5): x + 486.

——, 1930. — Ophiures recueillis par le docteur Th. Mortensen dans les mers d'Australie et dans l'Archipel Malais. *Vidensk. Meddr. dansk naturh. Foren.* 89: 1-295.

LJUNGMAN A. V., 1867. — Ophiuroidea viventia huc usgue cognita enumerat. *Ofvers. K. Vetensk.-Akad. Forh.* 23(9): 303-336.

——, 1871. — Forteckning ofver uti Vestindien of Dr. A. Goes samt under Korvetten Josefinas expedition i atlantiska oceanen samlade Ophiurider. *Ofv. Kongl. Vet-AK Forh.* 6: 615-657.

LORIOL, P. de., 1893a. — Echinodermes de la Baie d'Amboine. *Revue suisse Zool.* 1: 359-426.

——, 1893b. — Catalogue raisonné des echinodermes. III. Ophiurides et astrophytides. *Mem. Soc. Phys. et Hist. nat. Genève* 32, 1(3): 1-63.

LÜTKEN, C. F., 1856. — Bidrag til kundskab om Slangestjernerne. II. Ovesigt over de vestindiske Ophiurer. *Vidensk. Meddr. dansk. naturh. Foren* 1: 1-19.

——, 1869. — Additamenta ad Historiam Ophiuridarum. 3. Beskrivende og kritiske Bidrag til kundskab om Slangestjernerne. *K. danske Vidensk. Selsk. Skr.* 5(8): 24-109.

LYMAN, T., 1874. — Ophiuroidea and Astrophytidae, old and new. *Bull. Mus. comp. Zool.* 3: 221-272.

——, 1879. — 'Challenger' Ophiuroidae and Astrophytidae. pt. 2. *Bull Mus. comp. Zool.* 5: 17-83.

——, 1880. — A structural feature hitherto unknown among echinodermata found in deep-sea Ophiurans. *Anniv. Mem. Boston Soc. nat. Hist.*: 1-12.

——, 1882. — Report on the Ophiuroidea. *'Challenger' sci. Results: Zoology*, 5: 1-386.

MARSH, L. M., and MARSHALL, J. I., 1983. — Some aspects of the zoogeography of north-western Australian echinoderms (other than holothurians). *Bull. mar. Sci.* 33(3) 671-687.

MORTENSEN, T., 1924. — Echinoderms of New Zealand and the Auckland—Campbell Islands. II. Ophiuroidea. *Vidensk Meddr. dansk. naturh. Foren.* 77: 91-177.

——, 1940. — Echinoderms from the Iranian Gulf. Asteroidea, Ophiuroidea and Echinoidea. *Dan. scient. Invest. Iran*, part 2: 55-110.

PETERS, W., 1851. — Ubersicht der von ihm an der Kuste von Mossambique eingesammelten Ophiuren, unter denen sich zwei neue Gattungen befinden. *Ber. K. preuss. Akad. Wiss.*: 463-466.

ROWE, F. W. E., and VAIL, L. L., 1982. — The distributions of Tasmanian echinoderms in relation to southern Australian biogeographic provinces. *In*: J. M. LAWRENCE, (ed.), *Echinoderms: Proceedings of the International Conference, Tampa Bay*: 219-225. Rotterdam: A. A. Balkema.

Pycnodithella harveyi, a new Australian Species of the Tridenchthoniidae (Pseudoscorpionida: Arachnida)

CLARICE M. A. KENNEDY

KENNEDY, C. M. A. *Pycnodithella harveyi*, a new Australian species of the Tridenchthoniidae (Pseudoscorpionida: Arachnida). *Proc. Linn. Soc. N.S.W.* 110 (3), (1988) 1989: 289-296.

A new species of the genus *Pycnodithella* Beier, *P. harveyi* is described from the Sydney region. It is only the second known species of the genus and is characterized by its relatively small size and a distinctly reticulated carapace.

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INTRODUCTION

The family Tridenchthoniidae Balzan 1891 is at present represented by 16 genera including approximately 70 species. Of these, only two species namely: *Anaulacodithella australica* Beier and *Heterolophus australicus* Beier, have been described from Australia, the remainder are mostly confined to SE Asia and Africa. The species described herein is only the second known species of the genus *Pycnodithella* Beier and its first Australian representative.

Measurements are based on the examination of 10 specimens of each stage made in accordance with those discussed in Chamberlin (1931). Those in parentheses are the female and follow those of the male.

Abbreviations for cheliceral trichobothria and setal formulae follow those devised by Chamberlin (1931). All specimens are preserved in spirit.

SYSTEMATIC DESCRIPTION

TRIDENCHTHONIIDAE Balzan 1891

Remarks: Chamberlin and Chamberlin (1945) state that the name Dithidae, which has been used by various authors, is a synonym of the Tridenchthoniidae.

1947 ***Pycnodithella*** Beier

Type species: *Pycnodithella abyssinica* (Beier) 1944

Emended diagnosis: Dorsum of chelal hand without transverse furrow; fixed chelal finger with 8 trichobothria, *et* near *ds*, distinctly separated from *it/est*; movable chelal finger with acute teeth extending to finger base; intercoxal tubercle absent.

Remarks: The genus *Pycnodithella* was erected by Beier (1947: 287) solely on the basis of the position of the trichobothria *et* in relation to the double setae *ds*. The discovery of a new species, here assigned to *Pycnodithella* has therefore necessitated the emended diagnosis for the genus.

Pycnodithella differs from *Verrucadithella* Beier 1931 in that the dorsum of the chelal hand does not possess a transverse groove.

Anaulacodithella (Beier) 1944 is distinguished from *Pycnodithella* in that the trichibothria *et*, *it* and *est* of the fixed chelal finger are grouped togoether, distinctly separate from the double setae *ds* and that the teeth of the movable chelal finger, proximal to the trichobothria *st*, are replaced by a wavy lamella extending to the finger base.

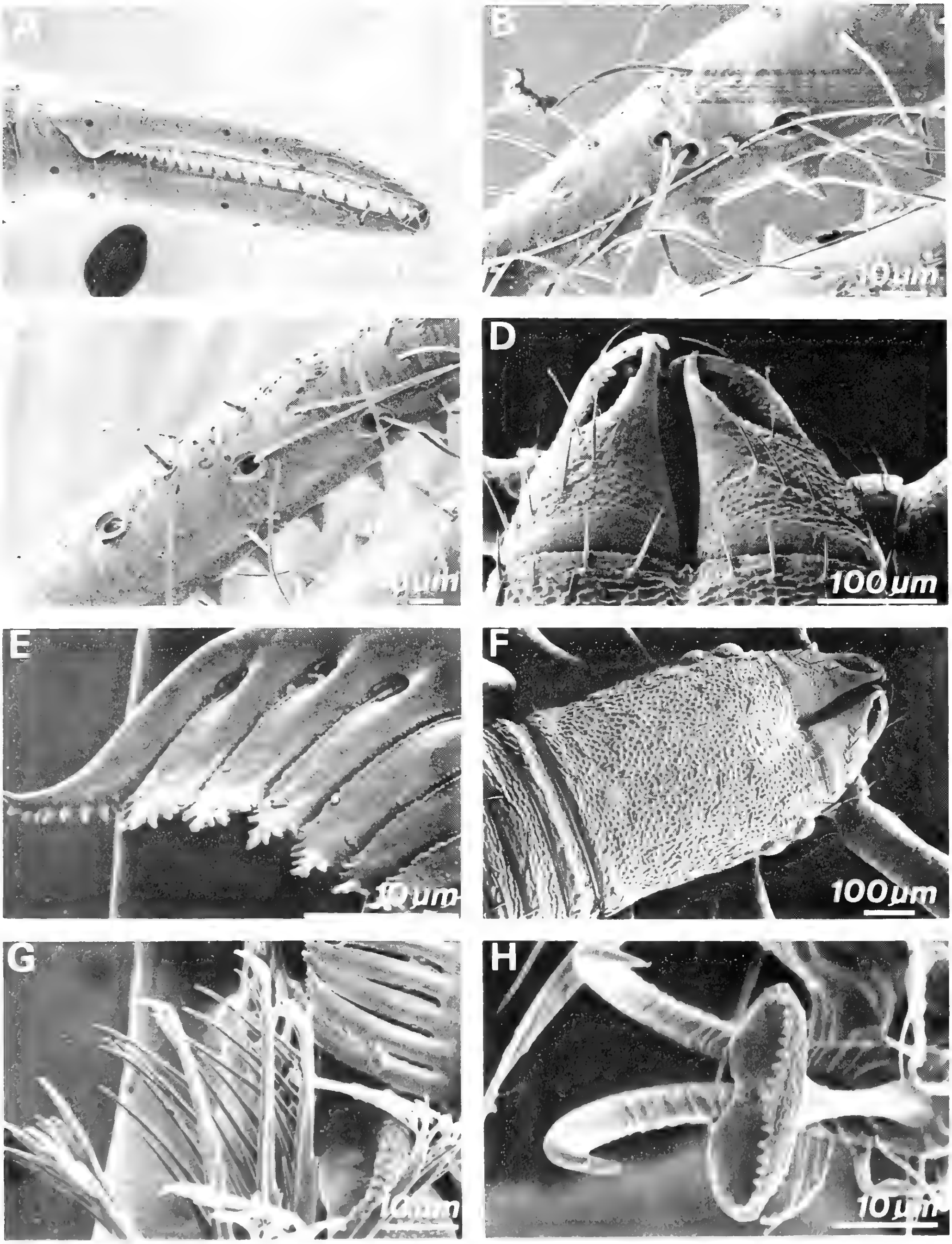

Fig. 1. Scanning electron micrographs. *Pycnodithella harveyi* n. sp., male paratype: **A**, lateral aspect of left chela; **B**, fixed chelal finger showing trichobothria *et* near *ds*; **C**, movable chelal finger showing trichobothria *t*, *st* and *sb* equidistant; **D**, chelicerae, dorsal aspect; **E**, distal lamellae of serrula exterior; **F**, Carapace showing conspicuous reticulate sculpture and well developed eyes; **G**, unilateral pinnate blades of flagellum; **H**, pretarsus.

Pycnodithella harveyi sp.nov.

(Fig. 1, Fig. 2, Fig. 3, Fig. 4)

Etymology: This species is named in honour of Dr M. S. Harvey in recognition of the great contribution he has made to the knowledge of the Pseudoscorpion fauna in Australia.

Holotype: ♂, Australian Museum, Sydney (KS 17441).

Type locality: Macquarie University campus, North Ryde, 13.5km NW of Sydney G.P.O., N.S.W.; 33°47′S, 151°07′E, in litter, 17.vi.85, C. Kennedy.

Paratypes: same data as holotype, Australian Museum, 6♂ (KS 17442), 6♀ (KS 17443), 6 nymphs (KS 17444). Distribution to various other museums in progress.

Diagnosis: Trichobothria *t*, *st* and *sb* equidistant (Fig. 1**C**); fixed chelal finger with 20-22, movable chelal finger with 16-18 acute, well-spaced teeth. Carapace conspicuously reticulate; chela (with pedicel) 0.59-0.64 (♂), 0.64-0.73 (♀) mm in length, 4.20-5.08 (♂) 4.0-4.70 (♀) x longer than broad; 1st and 2nd pedal coxae each with 4 medial coxal spines.

Description: Adults. Colour dark brown; pleural membrane cream, smooth; dorsal surface of cephalothorax with conspicuous reticulate sculpture extending to cornea of eyes and tergites (Fig. 1**F**), fields of reticulation deeply depressed on carapace, somewhat shallow on tergites. Pedipalpal trochanter with gently rounded anterior margin, L/W ratio 1.10-1.71 (♂), 1.20-1.80 (♀), femur straight increasing in width distally 3.02-2.50 (♂), 3.83-4.80 (♀), tibia pyriform, curved towards tibio-femoral insertion, 1.90-2.30 (♂), 1.75-2.25 (♀); chela distally setose, very slightly papillate dorsally, smooth ventrally with 20-30 short, acuminate setae, chela (with small pedicel) 4.21-5.08 (♂), 4.05-4.71 (♀), chela (without pedicel) 4.0-4.90 (♂), 3.52-4.50 (♀) x longer than broad. Fixed finger with 8 trichobothria, *et* near *ds* and distinctly separate from *it/est* (Fig. 1**B**), movable finger with 4 trichobothria (Fig. 1**A**), marginal teeth acute, distinctly separated on both fingers, progressively smaller proximally, never contiguous, 20-22 fixed finger, 16-18 movable finger (Fig. 3**R**); 2 minute teeth at base of terminal teeth precede marginal rows. Chelicerae large, stout, fixed finger dorsally papillate except distally, broad smooth band along posterior margin, 6-8 setae, *ls* absent, 10 minute antrorse teeth, first large; movable finger slender, galeal seta anterior to 7-8 marginal teeth, terminal tooth large, erect, others progressively very small and antrorse, galea absent. (Fig. 1**D**). Serrula exterior with 16-17 (♂), 15-16 (♀) lamellae (Fig. 1**E**); serrula interior with 8-10 thick, blunt lamellae, serrate margin. Flagellum with 8-10 slender, unilaterally pinnate blades of sub-equal length, distally divided into 3-4 short spines that are bent at an obtuse angle with respect to the blades and are directed towards the midline; 6-7 long 'spines' well-spaced along the upper two thirds of the blades point in the same direction (Fig. 1**G**); base of blades stalk-like. Carapace (Fig. 1**F**) anterior margin serrate, median blunt vestigial epistome (Fig. 3**P**); setae spine-like 8:8-10:50-60 (♂), 8:8-10:40-50 (♀); two well-developed eyes; L/W ratio 1.0-1.16 (♂), 0.77-1.0 (♀) x longer than broad. Tergal chaetotaxy: ♂ 12-14: 12-14: 14-16: 14-16: 15-16: 15-16: 16-18: 15-16: 10-12: 10: 8-10: 2; ♀ 12-14: 12-14: 12-14: 14-16: 14-16: 14-16: 13-16: 12-15: 13-14: 10-12: 10: 2, uniseriate. Coxae: 1st pedal coxae with anterior mesial process; 1st and 2nd pedal coxae each with 4 short medial coxal spines transversely incised into finger-like projections distally (Fig. 2**I**, **J**), base of spine thick; intercoxal tubercle absent. Coxal chaetotaxy: ♂ 2: 4-5: 6-8, 0:6-8:4, 0: 6-8: 4-5, 0: 6-8: 7-10, 0: 6-8: 8-11; ♀ 2: 6: 5-6, 0: 4-6: 4-6, 0: 4-6: 4-8, 0: 4-6: 8, 0: 4-6: 10-12, 8-10 long acuminate setae on posterior border. Male genitalia: consisting of complex series of sclerotized apodemes and rods, dorsal anterior apodeme appears brush-like; ejaculatory canal atrium cup-shaped and anterior to genital armature (Fig. 4**V**). Fig. 4**T** shows the three dimensional structure of the genitalia. Chaetotaxy: ♂

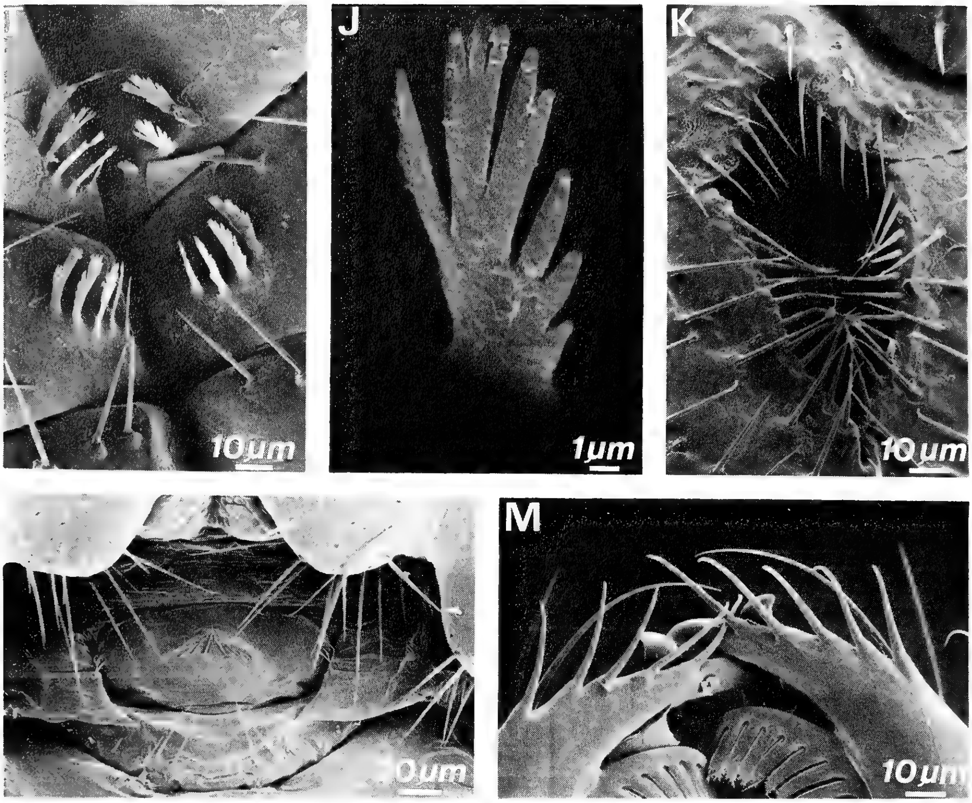

Fig. 2. Pycnodithella harveyi n. sp. **I**, male-coxal spines; **J**, enlargement of distal portion of one coxal apine; **K**, male genital region, external aspect; **L**, female genital region, external aspect; **M**, tritonymph showing multiple simple galeae.

genital plate medially in the form of a diamond; anterior operculum with 5 marginal, long acuminate setae each side projecting into open cavity, posteriorly a row of shorter setae running parallel to the former; posterior operculum: 11 marginal acuminate setae each side, closely spaced, projecting into lower part of cavity and converging centrally to enclose cavity in kind of grill, posteriorly, a row of widely-spaced setae extending beyond operculum margin; posterior to the former a row of 4 shorter setae behind which is one very long seta (Fig. 2**K**). Female genitalia: strongly sclerotic with pronounced thickenings; thin irregularly-shaped transverse median cribriform plate; numerous minute platelets scattered within sclerotization; spiracles obliquely situated with well defined stigmatic plates (3 setae each) and characteristic for family (Fig. 4**W**) spermathecae absent. Chaetotaxy: anterior operculum with 6-8 centrally located setae converging to form a pyramid; posterior operculum with 15-17 very short setae on posterior border (Fig. 2**L**). Sternal chaetotaxy ♂ 4-8 weakly divided, 0:18-20: 23-25: 12-14: 18-20: 16-20: 16-18: 14-16: 14-16: 12-14: 10-12: 2, sternites 4-12 uniseriate; ♀ 4-8 weakly divided, 0: 16-18: 12-14: 8-10: 14-16: 12-16: 14-16: 14-18: 14-15: 12-14: 10-12: 2, sternites 3-12 uniseriate. Pretarsus: claws obliquely ridged, curving over a trumpet-shaped arolium with delicate serrate rim (Fig. 1**H**). Heterotarsate. Dimensions (mm): body length 1.-1.16 (1.18-1.51); pedipalps: trochanter 0.14-0.16/0.09-0.10 (0.12-0.18/0.09-0.12), femur 0.37-0.45/0.09-0.12 (0.41-0.52/0.10-0.12), tibia 0.19-0.27/0,10-0.12 (0.21-0.27/0.10-0.12), chela (with

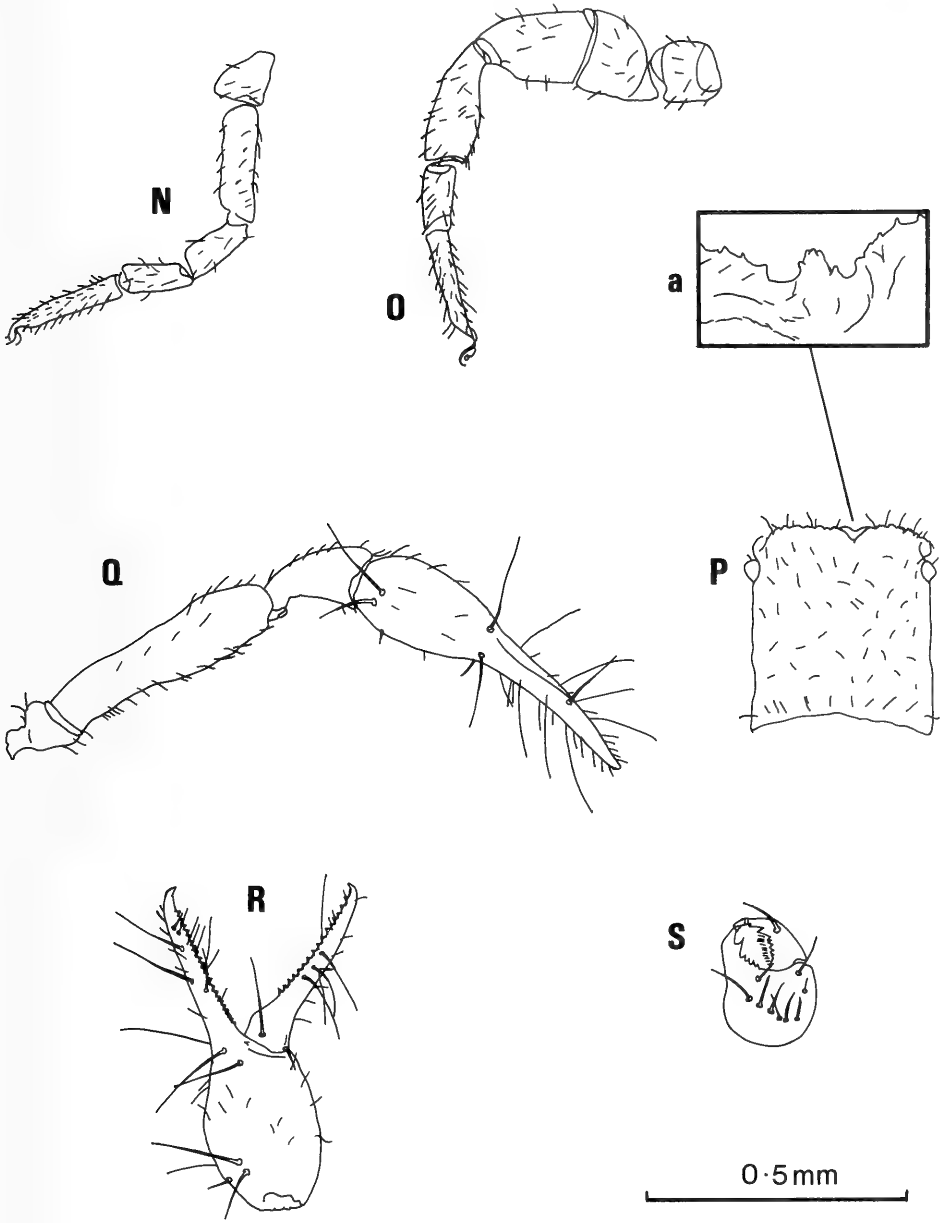

Fig. 3. Pycnodithella harveyi n. sp., male paratype: **N**, leg I; **O**, leg IV; **P**, carapace, dorsal aspect — inset **a**, epistome not clearly defined in light microscopy) traced from scanning electron micrograph x 1700; **Q**, left pedipalp, dorsal aspect; **R**, right chela, lateral aspect; **S**, right chelicera, dorsal aspect.

pedicel) 0.59-0.64/0.12-0.15 (0.64-0.73/0.14-0.18), chela (without pedicel) 0.55-0.60/0.12-0.15 (0.60-0.70/0.14-0.18), movable finger length 0.30-0.36 (0.36-0.43); chelicera 0.19-0.25/0.10-0.12 (0.18-0.27/0.12-0.16), movable finger length 0.12-0.14 (0.14-0.18); carapace 0.36-0.43/0.34-0.39 (0.37-0.47/0.39-0.48); anterior eye 0.052-0.054 (0.052-0.056), posterior eye 0.046-0.048 (0.048-0.05); leg I: coxa width 0.09-0.14 (0.09-0.14), trochanter

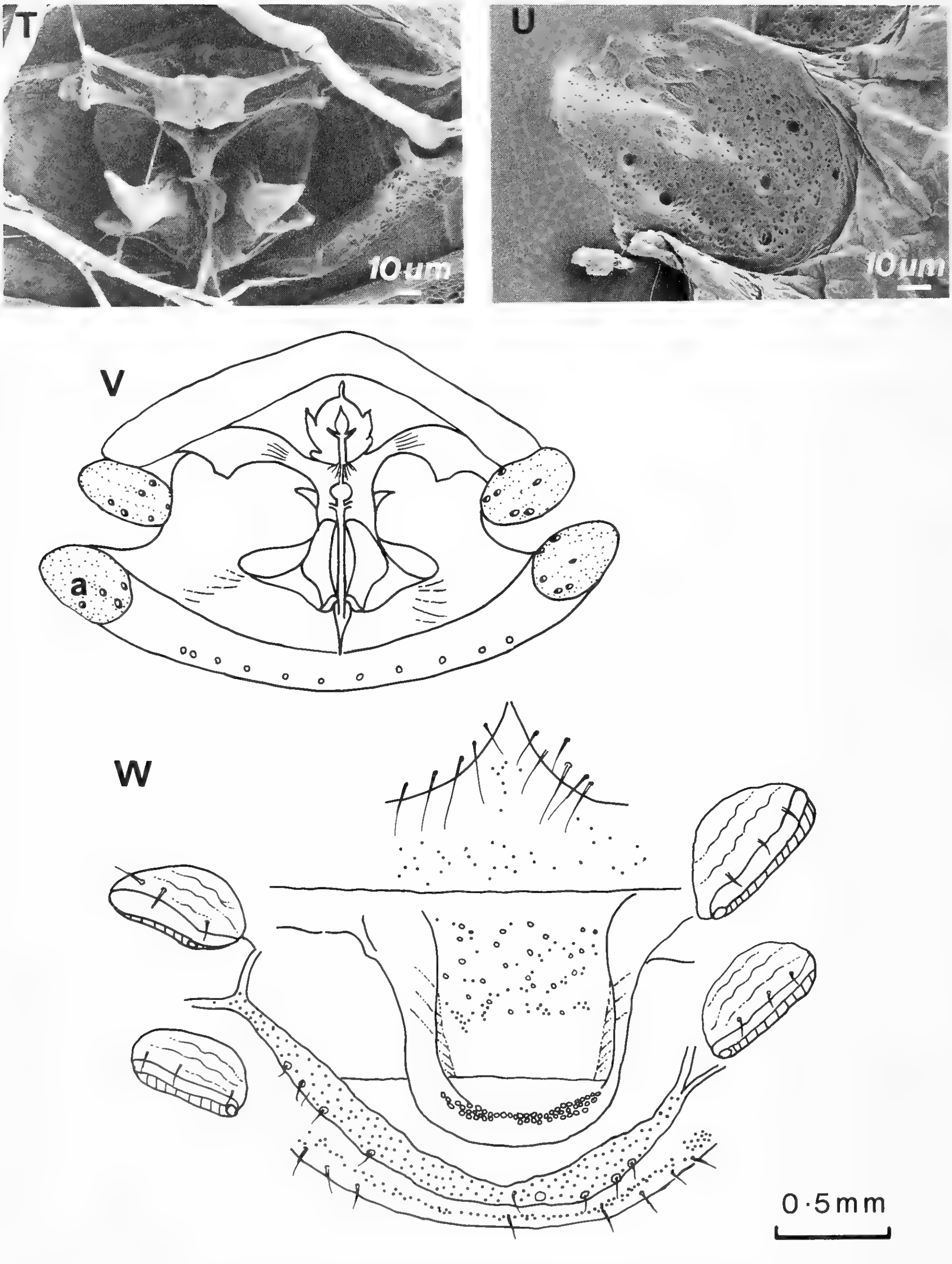

Fig. 4. Pycnodithella harveyi n. sp., paratypes: **T**, male genitalia, ventral aspect; **U**, sclerotic, perforated plate designated **a** in **V**. **V** male genitalia and associated sternites; **W**, female genitalia and associated sternites.

0.09-0.12/0.07-0.10 (0.10-0.18/0.09-0.10), basifemur 0.18-0.23/0.03-0.05 (0.10-0.27/0.03-0.05), telofemur 0.10-0.18/0.03-0.05 (0.10-0.18/0.03-0.05), tibia 0.09-0.14/0.03-0.04 (0.10-0.16/0.03-0.05), miotarsus 0.16-0.21/0.03 (0.12-0.19/0.02-0.03); leg IV: coxa width

0.09-0.10 (0.10-0.12), trochanter 0.10-0.16/0.09-0.11 (0.15-0.91/0.09-0.12), basifemur 0.16-0.18/0.07-0.12 (0.12-0.27/0.09-0.12), telofemur 0.18-0.21/0.07-0.09 (0.18-0.21/0.07-0.12), tibia 0.16-0.21/0.06-0.08 (0.12-0.27/0.07-0.09), metatarsus 0.09-0.14/0.03-0.05 (0.12-0.15/0.03-0.05), telotarus 0.18-0.21/0.03-0.04 (0.18'0.21/0.03).

Tritonymphs. Pedipapal trochanter 1.0-1.70, femur 3.10-4.57, tibia 1.33-1.80, chela (with pedicel) 3.50-4.60, chela (without pedicel) 3.25-4.10 x longer than broad. Fixed finger with 7 tricobothria, *isb* absent, movable finger with 3 trichobothria, *b* absent. Chelicera with 5 simple galea (Fig. 2**M**), serrula exterior of chelicera with 13-14 lamellae. Carapace with 4: 10: 25-35 setae; 0.82-1.0 x longer than broad. Tergal chaetotaxy: 10-12: 10-12: 10-12: 8-10: 8-10: 8-10: 8-10: 8-10: 8-10: 8-10: 4-6: 2. Sternal chaetotaxy: 8-10: 8-10: 8: 7-8: 8: 8-10: 8-10: 8-10: 7-8: 5-8: 2-3: 2. Coxal chaetotaxy: 1st pedal coxae with mesial process, 1st and 2nd coxae each with 4 medial coxal spines, 0: 4-5: 3, 0: 4-5: 3, 0: 4-5: 7, 0: 6-8: 7-8.
Dimensions (mm): body length 0.90-0.99; pedipalps: trochanter 0-10-0.14/0.07-0.09, femur 0.27-0.36/0.07-0.09, tibia 0.12-0.18/0.09-0.10, chela (with pedicel) 0.41-0.52/0.1-0.14, chela (without pedicel) 0.39-0.50/0.10-0.14, movable chelal finger 0.21-0.32; carapace 0.30-0.36/0.32-0.39.

Deutonymphs. Pedipalpal trochanter 1.0-1.28, femur 2.57-3.85, tibia 1.28-1.77, chela (with pedicel) 4.0-4.55, chela (without pedicel) 3.90-4.55 x longer than broad. Fixed finger with 6 trichobothria *ist* and *isb* absent, movable finger with 2 trichobothria, *sb* and *b* absent. Chelicerae with 4 simple galea. Serrula exterior with 11-12 lamellae. Carapace 3: 8: 20-30 setae, 0.87-0.10 x longer than broad. Tergal chaetotaxy: 8-10: 6-8: 6-8: 8-10: 8-10: 6-8: 5-7: 5-8: 4-5: 4-5: 3-4: 2. Sternal chaetotaxy: 1-2: 1-2: 5-6: 5-6: 5-6: 5-6: 5-6: 5-6: 4-5: 4-5: 3-4: 2. Coxal chaetotaxy: 1st pedal coxae with mesial process. 1st and 2nd pedal coxae each with 4 short medial coxal spines, 0: 2-4: 1, 0: 3-4: 2, 0: 2-4: 2, 0: 2-4: 3.
Dimensions (mm): body length 0.70-0.73. Pedipalps: trochanter 0.07-0.09/0.06-0.08, femur 0.18'0.27/0.07-0.08, tibia 0.09-0.16/0.07-0.09, chela (with pedicel) 0.37-0.43/0.09-0.10, chela (without pedicel) 0.36-0.41/0.09-0.10, movable finger length 0.19-0.25; carapace 0.23-0.30/0.25-0.32.

Protonymphs. Present indications suggest there is no free living protonymph stage. The question as to whether the embryonic protonymph stage follows a pattern of development similar to that of *Chthonius tetrachelatus* Preyssler (Weygoldt, 1968a,b), or if indeed this stage is suppressed in the Australian species, is at present under investigation.

Comparisons: *P. harveyi* n. sp. differs from *P. abyssinica* (Beier) 1947 in the sculpture of the carapace which is conspicuously reticulate in contrast to the finely granulated type species. The trichobothria *t*, *st*, *sb* in the new species are equidistant (Fig. 1**C**), as compared with the situation in *P. abyssinica* where *st* of the movable chelal finger is clearly nearer *sb* than *t*. The new Australian species is also distinctly smaller in most respects than *P. abyssinica* and has fewer teeth in both chelal fingers.

ACKNOWLEDGEMENTS

I wish to express my thanks to Dr P. D. Hillyard (British Museum (Natural History), London) for the loan of type material, to Dr M. S. Harlvey (Museum of Victoria, Melbourne) for his guidance and comments offered on the manuscript and to Mr R. J. Oldfield, Macquarie University, for advice in respect to photographic layout.

References

BALZAN, L., 1891 — Voyage de M. E. Simon au Venezuela: Chernetes (Pseudoscorpiones). *Ann. Soc. entomol. France*, 60: 504-505, 509.

BEIER, M., 1944 — Über Pseudoscorpioniden aus Östafrika. *Eos Madr.*, 20: 173-212.

——, 1947 — Zur Kenntnis der Pseudoscorpioniden-fauna des südlichen Afrika, insbesonders der südwestund Trockengebiete. *Eos Madr.*, 23: 285-339.

CHAMBERLIN, J. C., 1931 — The arachnid order Chelonethida. *Stanford Univ. Publs Biol. Sci.* 7: 1-284.

——, and CHAMBERLIN, R. V., 1945 — The genera and species of the Tridenchthoniidae (Dithidae): a family of the arachnid order Chelonethida. *Bull. Univ. Utah* 35(23), Biol. ser. 9(2).

WEYGOLDT, P., 1968a — Vergleichend-embryologische Untersuchungen an Pseudoscorpionen IV. *Zeits. für Morph. der Tiere* 63: 111-154.

——, 1986b — *The Biology of Pseudoscorpions*. Cambridge, Mass.: Harvard Univ. Press.

PROCEEDINGS
of the

LINNEAN SOCIETY

of
NEW SOUTH WALES

VOLUME 110
NUMBER 4

A Study of the Crustacean Zooplankton of Six Floodplain Waterbodies of the Lower Hunter Valley, N.S.W.

B. V. TIMMS

TIMMS, B. V. A study of the crustacean zooplankton of six floodplain waterbodies of the lower Hunter Valley, N.S.W. *Proc. Linn. Soc. N.S.W.* 110 (4), (1988) 1989: 297-306.

Thirteen species of eulimnetic entomostracans occurred in the waterbodies with *Boeckella fluvialis*, *Calamoecia lucasi*, *Mesocyclops albicans*, *Daphnia carinata* and *Moina micrura* dominant. Momentary species composition averaged 1.8 calanoid species, 1.4 cyclopoid copepod and 2.8 cladoceran species. Numerically, calanoids and cladocerans dominated (42% each). The low number of cladoceran species and the importance of calanoids are unusual in a world context, so possible reasons for these are explored. Most differences between lagoons are explained in terms of relative habitat stability and the presence/absence of predators.

Seasonal variation in total numbers was erratic. All copepods were perennial, *Daphnia carinata*, *D. lumholtzi* and *Bosmina meridionalis* were almost perennial, while the remaining cladocerans were distinctly seasonal. Members of the congeneric pairs *Diaphanosoma excisum — D. unguiculatum*, *Daphnia carinata — D. lumholtzi*, and *Ceriodaphnia cornuta — C. 'dubia'* peaked at different times.

Four of the waterbodies dried periodically, but zooplankton populations recovered quickly on refilling, much faster than the colonization of new sites. Successional sequences depended on season, but generally cyclopoids and *Moina micrura* were fast colonizers, followed by *Boeckella fluvialis*, *Daphnia carinata*, then *Bosmina meridionalis*, and lastly *Calamoecia lucasi* and *Daphnia lumholtzi*.

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manuscript received 4 August 1987, accepted for publication 17 February 1988.

KEY WORDS: Calanoida, Cyclopoida, Cladocera, seasonal distribution, community structure, plankton predators, colonization.

INTRODUCTION

Compared with other aquatic communities, the crustacean zooplankton of Australian lakes is relatively well known. There is information on taxonomy and distribution of the major components (e.g. Bayly, 1961, 1964, 1966, 1979, on calanoid copepods; Bayly and Morton, 1978, Morton, 1985, on some cyclopoid copepods; Smirnov and Timms, 1983, on cladocerans), and on the association of species in various areas (Mitchell, 1986; Shiel *et al.*, 1982; Timms and Morton, 1988). Study continues on the value and methodology of conceptualizing associations and on the relative importance of physicochemical and biological factors in determining species composition and seasonal change. Earlier work used and misused the statistic 'momentary species composition' and concentrated on the influence of physiocochemical parameters (e.g. Timms, 1970a), though the role of competition was not completely ignored (e.g. Bayly, 1966: Jolly, 1966). More recently the effect of vertebrate and invertebrate predation has been highlighted (Geddes, 1986; Grant and Bayly, 1981; Reynolds and Geddes, 1984) and new methods devised to depict species composition (Mitchell, 1986).

Most of these interpretations have been based on spot sampling or on short-term studies with some narrow goal in mind. An alternative approach is to monitor plankton over many years and to interpret general trends. Such studies, e.g. Jolly (1966) on the Sydney reservoirs, lack the rigour of specific goal short-term studies, but they can provide useful data. For instance, long-term studies are more likely to record all species at a given site and provide a more accurate assessment of the 'average' plankton community.

Also such studies are able to record in proper context the effect of irregular events such as floods and droughts.

In this paper the crustacean zooplankton of six small floodplain waterbodies of the lower Hunter Valley have been studied monthly for just over 5 years. This period encompassed two droughts and a number of minor floods. With the broadscale distribution of crustacean zooplankters in the region known (Timms, 1970a) and comparative seasonal data available for nearby reservoirs (Timms, 1970b), the aim of this study is to document the long-term composition and variability of plankton in natural sites in mid-eastern Australia and to note the major influencing factors.

STUDY SITES AND METHODS

Six floodplain waterbodies of the lower Hunter River near Maitland were sampled monthly from October, 1979 to December 1984. Geomorphically they are blocked valley lakes, but locally they are called 'lagoons', a descriptor used in Australia for any small inland waterbody, so this practice is adopted here. Their location, geomorphic parameters and salient physicochemical features are given in Timms (1987b). Lagoons 1a and 1b contained water throughout the study, and Lagoon 3 was nearly permanent, only drying for 3 out of the 63 months. The other lagoons were intermittently present — Lagoon 2 was dry for a total of 27 months, Lagoon 4 for 26 months and Lagoon 5 for 31 months (see Timms, 1987b: fig. 4). All lagoons filled from their local catchment. On occasions macrophytes grew too extensively to allow open water sampling in Lagoon 3 and less frequently in Lagoon 2.

On each sampling occasion, a conical net 30.5cm in diameter and mesh size 159μm was used to collect zooplankton from open water. If the site was >40cm deep an oblique haul from near the bottom to the surface was taken from a boat, but if the depth was <40cm deep a horizontal tow was taken by wading through the lagoon. In both cases the net was towed at approximately 20cm sec^{-1} for 2 minutes over 25m, thus filtering 1820L at most, but almost certainly much less (Bottrell *et al.*, 1976). The method is semi-quantitative at best, but consistent. Samples were preserved in 5% formalin. Subsamples were taken from each collection so that about 1000 individuals were enumerated. Plankters were assigned to species, though this was incomplete for cyclopoid copepods (small *Mesocyclops albicans* were included with *Thermocyclops decipens* and the latter were lumped with *Eucyclops* spp.). Where two species of calanoid copepod co-occurred, copepodites were included in species totals according to the ratio of adult individuals identified for the species present.

RESULTS

(a) Species Composition and Community Structure

Altogether 13 eulimnetic entomostracans, comprising 3 calanoid copepods, 2 cyclopoid copepods and 8 cladocerans occurred in the 6 lagoons (Table 1). Eight littoral species (2 cyclopoids, 2 ostracods, 3 chydorid cladocerans and *Simocephalus*) sometimes were collected from open waters, but generally in small numbers. *Eucyclops* spp. may have occurred in lagoons other than No. 3, but it is consistent they should be found in the site with the best developed littoral macrophytes. In addition shrimp larvae (?*Paratya australiensis*) occurred in Lagoons 1a, 1b, and 3, mainly in summer, and a number of rotifers, including *Brachionus* spp., *Keratella* sp. and *Asplanchna* sp., were common in summer-autumn. Species composition was similar, but not identical, in each lagoon (Table 1).

The presence of possible plankton predators was also noted. European Carp (*Cyprinus carpio* L.) was common in Lagoon 1b and colonized Lagoon 1a during 1983, but were

TABLE 1

Relative Importance of Entomostracan Zooplankters in the Lagoons

		Lagoons					
	Species	1a	1b	2	3	4	5
1.	*Diaphanosoma excisum* Sars	3.4	4.3	1.3	4.4	1.6	—
2.	*Diaphanosoma unguiculatum* Gurney	2.8	2.2	0.4	0.6	2.6	1.9
3.	*Moina micrura* Kurz	9.8	12.4	5.2	4.7	9.5	11.2
4.	*Bosmina meridionalis* Sars	2.9	7.7	3.4	2.2	4.4	0.7
5.	*Daphnia carinata* King	14.0	3.6	23.4	6.6	22.3	28.0
6.	*Daphnia lumholtzi* Sars	2.8	5.9	—	2.3	—	—
7.	*Ceriodaphnia cornuta* Sars	3.6	3.6	0.5	3.3	0.3	0.6
8.	*Ceriodaphnia 'dubia'* Richard	2.2	5.2	2.7	5.3	6.7	1.0
9.	Chydorids+	0.2	0.4	1.7	1.1	0.3	0.7
10.	*Simocephalus vetulus elisabethae* (King)	—	—	0.2	—	—	—
11.	*Newnhamia fenestrata* King	—	—	2.0	—	—	—
12.	*Cyprinotus fuscus* Henry	—	—	0.8	—	0.2	1.6
13.	*Boeckella fluvialis* Henry	12.0	8.4	18.7	21.5	14.4	25.7
14.	*Boeckella triarticulata* Thomson	—	—	—	—	—	1.4
15.	*Calamoecia lucasi* Brady	28.1	30.0	17.6	38.7	23.1	10.4
16.	*Mesocyclops albicans* (Smith)	12.0	10.3	15.0	6.4	12.4	11.8
17.	*Thermocyclops decipiens* (Kiefer)	6.2	6.1	7.1	3.0	2.2	5.0
18.	*Eucyclops* sp. nov.	—	—	—		—	—
19.	*Eucyclops* sp. prob. *euacanthus* (Sars)	—	—	—		—	—

* Calculated by averaging percent composition for each month in each lagoon.

\+ includes *Chydorus sphaericus* s.l. O. F. Müller, *Dunhevedia crassa* King, and *Alona diaphana* King.

still not common by December 1984. Mosquito Fish (*Gambusia affinis* Baird and Girard) were numerous in Lagoons 1a, 1b and 3. Notonectids (*Anisops* spp.,) occurred in all lagoons, particularly in Lagoons 2, 4 and 5, and were most common November to April (Fig. 2). No *Chaoborus* were ever caught in plankton tows or in a few Ekman grab samples taken in a benthic study (author, unpublished).

The relative importance of species varied between sites (Table 1). The main differences were between the permanent to near-permanent lagoons (Nos. 1a, 1b, 3) which also had fish and the intermittently-present lagoons (Nos. 2, 4, 5) which lacked fish. *Daphnia lumholtzi* was absent from the latter group and *Calamoecia lucasi*, *Diaphanosoma excisum*, *Ceriodaphnia cornuta*, were less common in them, though the differences may not be significant given the small number of sites. Three species were restricted to these intermittently present lagoons — the ostracods *Cyprinotus fuscus* found in all three and *Newnhamia fenestrata* in Lagoon 2 only, and *Boeckella triarticulata* in Lagoon 5 for just 3 months. On the other hand *Daphnia carinata* was most common in these lagoons. It and *Boeckella fluvialis* were least important in Lagoon 1b in which carp were abundant.

On average the six lagoons contain 1.8 calanoid species, 1.4 cyclopoid species and 2.8 cladoceran species (Table 2). There is seasonal variation in these averages, but it is erratic both between sites (Table 2) and between years (Fig. 1), especially for cladocerans. Of the three groups, however, cladocerans are more consistently present in permanent rather than intermittently present lagoons ($t = 9.5$, $P < 0.001$, $DF = 4$).

(b) **Seasonality**

Total numbers of zooplankton per month in each lagoon fluctuated *ca*10-100 fold with little apparent seasonal regularity (Fig. 1), but when data were averaged for each month in each lagoon, some general trends emerged (Fig. 2). In all lagoons numbers tended to be lowest in winter and highest in autumn. The two permanent lagoons (1a,

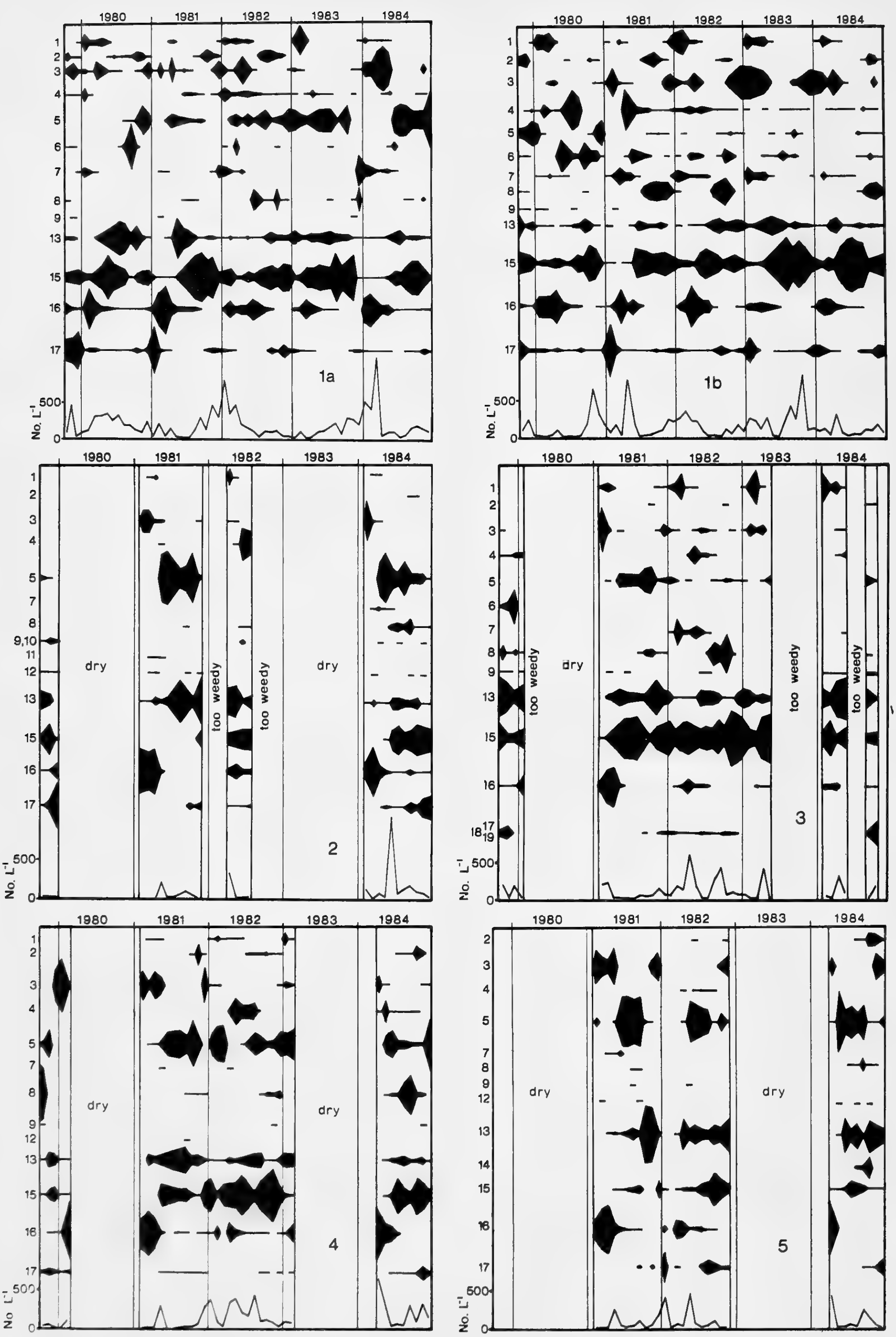

Fig. 1. Relative abundance and approximate total numbers per standardized collection of crustacean zooplankton in the six lagoons (**1a**, **1b**, **2**, **3**, **4**, **5**) for the period October 1979 to December 1984.

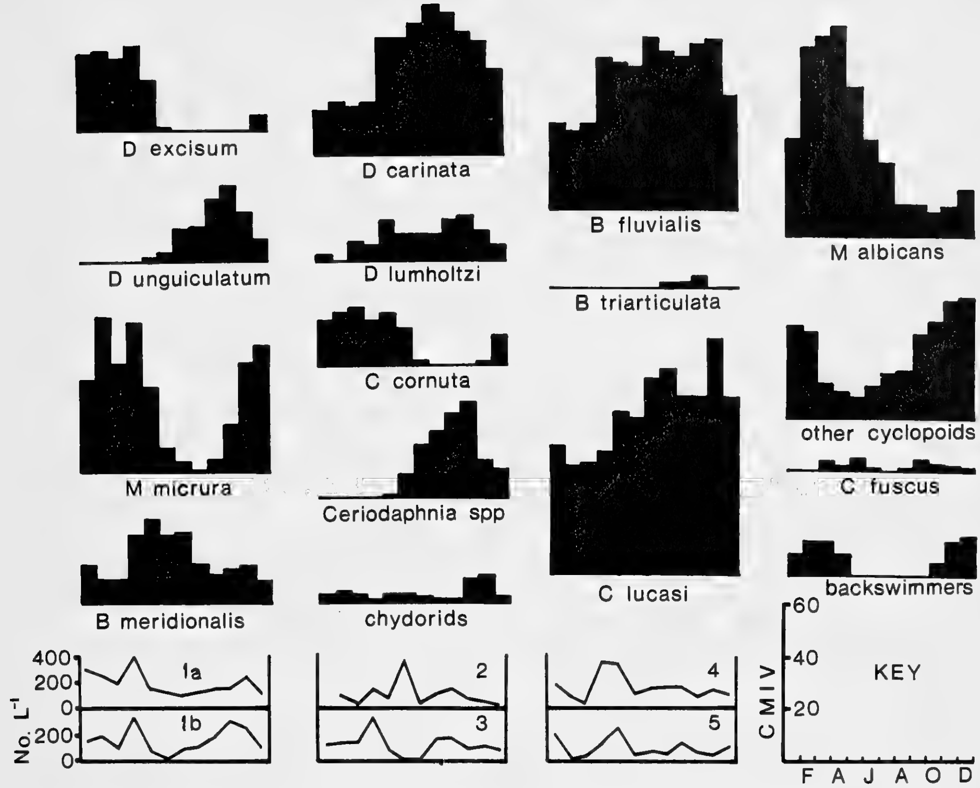

Fig. 2. Seasonal variation in the cumulative monthly importance values (CMIV) of various crustacean species and notonectids for the period October, 1979 to December, 1984. These are derived by giving each monthly occurrence of each species in each lagoon a numerical value (1 = when relative abundance < 2.5%, 2 = 2.5 - 10%; 3 = 10-25%; 4 = 25 - 50%; 5 = >50%) and then summing. Also shown is the average number of zooplankton per standardized collection for each month in each lagoon.

1b) had elevated numbers during October-November and in April. The intermittently-present lagoons (2, 4, 5) had only one major peak in April-June, and the near-permanent lagoon (3) had an intermediate pattern.

Kite diagrams of the percentage abundance of each species over the 63 month study period (Fig. 1) and histograms of cumulative monthly importance values (Fig. 2) show various patterns of seasonality. The calanoids *Boeckella fluvialis* and *Calamoecia lucasi* were perennial, with a period of minimal importance in summer-early autumn, i.e. December to March in *B. fluvialis* and January-April in *C. lucasi*. *Boeckella triarticulata* occurred only from August to October which does not indicate its full seasonal capabilities, as this occurrence is believed to be a failed colonization attempt (see later). Both *Mesocyclops albicans* and *Thermocyclops/Eucyclops* spp. were perennial or almost so (Fig. 2), but with distinct peaks from February to May and from September to February respectively. Three of the 8 eulimnetic cladocerans, *Daphnia carinata*, *D. lumholtzi* and *Bosmina meridionalis* may have been perennial (Fig. 2), though they were not continuously present in any lagoon (Fig. 1). *Daphnia carinata* peaked seasonally in May-October and *B. meridionalis* in April-July. The other 5 species were distinctly seasonal (Fig. 2) — *Diaphanosoma excisum* from January to May, *D. unguiculatum* from July to November, *Moina micrura* from November to May, *Ceriodaphnia cornuta* from December to July, and *C. 'dubia'* from

July to October. Fig. 2 suggests some overlap in the presence of each species in the three congeneric pairs of cladocerans, but this rarely happened in individual lagoons (Fig. 1). Littoral cladocerans tended to stray into open water in any month, but with a peak in spring, and the ostracod *Cyprinotus fuscus* was also recorded in almost any month, except in January, February and July.

(c) **Influence of Floods and Droughts**

No major river floods occurred during 1979-84, but there were a number of periods of heavy rainfall, local flooding and rapid rises in the levels of the lagoons (Timms, 1987b). No particular effect of these inflows was detected, though in general population peaks occurred in April-May, two months after peak seasonal rainfall.

The lagoons refilled after being dry on 7 occasions, twice each in Lagoons 2, 4 and 5 and once in Lagoon 3 (Fig. 1). Generally the order of response was *Moina micrura* $>$ *Mesocyclops albicans* $>$ *Boeckella fluvialis* $\lesseqgtr$ *Daphnia carinata*. On one occasion each *Bosmina meridionalis* and *Diaphanosoma excisum* reestablished quickly. *Boeckella fluvialis* typically established sizeable populations a month or so earlier than *Calamoecia lucasi*.

DISCUSSION

(a) **Species Composition**

Almost all of the species recorded in the six study sites are within their known distribution in northeastern N.S.W. (Smirnov and Timms, 1983; Timms, 1970a). The only exception is *Ceriodaphnia 'dubia'* but re-examination of most of the collections used for Timms (1970a) and (1970b) showed it indeed occurred in a few. More notable are some omissions. *Boeckella minuta* is absent, though common in reservoirs and some natural lakes in mid-eastern Australia, thus confirming its preference for newly-created habitat (Bayly, 1979; Timms, 1970a). *Gladioferens spinosus* is also absent, despite being present in the nearby Hunter River and in local reservoirs which draw their water from it (Timms, 1970b). It seems this species is dispersed almost exclusively through the aquatic medium (Timms, 1970b, 1973), but apparently conditions during major floods when the lagoons are in contact with the Hunter River are unsuitable for dispersal for other reasons.

Of the factors likely to affect species composition and seasonal distribution of crustacean zooplankton, some data are available on the degree of permanence of the lagoons (the major physicochemical difference between them — Timms, 1987b) and on the presence of fish and notonectids. Many differences between the 3 permanent and 3 intermittently-present lagoons (Table 1) can be explained by (a) the relatively poor colonization and recovery ability of *Calamoecia lucasi* (Maly, 1984a; Timms, 1970a, 1987a) and also of *Daphnia lumholtzi* (Timms, 1970a, 1987a) and hence their lesser importance (*C. lucasi*) or absence (*D. lumholtzi*) from the three intermittently present lagoons, and (b) the lagoons being dry when species such as *Diaphanosoma excisum*, *D. unguiculatum* and *Ceriodaphnia cornuta* are normally abundant in lagoons and reservoirs in the area (Fig. 1 and Timms, 1970b).

While no specific data are available on predation by fish in these lagoons, the relatively poor performance of the two largest species, *Daphnia carinata* and *Boeckella fluvialis* in the two lagoons with fish is consistent with the work by Geddes (1986) on zooplankton composition in farm dams, Hume *et al.* (1983) and Straskraba (1965) on carp diets and Lloyd (1986) on the influence of mosquito fish on zooplankton. Also the abundance of predatory notonectids in the lagoons from November to April probably has profound effects on abundances of many species (*cf.* Geddes, 1986). The decline in early summer of *Daphnia carinata* and possibly also of other large species such as *D.*

lumholtzi, *Diaphanosoma unguiculatum* and *Boeckella fluvialis* (Figs 1 and 2) could be explained by predation pressure by notonectids. Seasonal changes in the relative abundance of the smaller species, *Diaphanosoma excisum*, *Moina micrura*, *Ceriodaphnia* spp. and *Calamoecia lucasi* do not coincide with the abundance of notonectids (Fig. 2).

(b) **Seasonal variation**

Erratic seasonal variation in zooplankton numbers as seen in these lagoons is to be expected in small lakes (Pennak, 1949), though there is a trend towards late spring and autumn maxima as seen in larger reservoirs nearby (Timms, 1970b), The perennial occurrence of *Boeckella fluvialis*, *Calamoecia lucasi*, *Mesocyclops albicans* (formerly misidentified as *M. leuckarti* in Australia), *Daphnia carinata* and *Bosmina meridionalis* is consistent with results of other studies in southeastern Australia (Geddes, 1968, 1984: Jolly, 1966; Timms, 1970b: Walker and Hillman, 1977). *Daphnia lumholtzi* is almost perennial in these lagoons, but with a distinct minimal in summer, whereas in nearby reservoirs (Timms, 1970b) it was most abundant in summer and usually absent in winter. Its absence from the 3 shallower ephemeral lagoons studied here and from nearby reservoirs during low water levels (Timms, 1970b), suggests that other factors associated with low water levels may inhibit its development. The seasonal distribution of other species mirror those reported elsewhere in southeastern Australia. *Diaphanosoma excisum* is abundant in summer-early autumn (Timms, 1967, 1970b), *D. unguiculatum* is a spring species (Geddes, 1984; Shiel *et al.*, 1982; Walker and Hillman, 1977), *Moina micrura* blooms in summer (Geddes, 1968, 1984; Shiel *et al.*, 1982; Timms, 1970b) and *Ceriodaphnia cornuta* is also a summer species (Timms, 1970b). No comparative data are available for *Ceriodaphnia 'dubia'.* All species, perennial and seasonal, appear to be multivoltine.

(c) **Community Structure**

Zooplankton community structure is often described by the parameter momentary species composition (MSC), which is the number of species present at any one time (Pennak, 1957). Mitchell (1986) has challenged its value and validity, but most of the inadequacies are due to limited data bases. In the present lagoons this is not a problem as MSCs are based on many observations totalling 32-63 according to lagoon.

The average MSC in the six lagoons (Table 2) is within the range reported for lakes and ponds in southern Australia, though on a world comparative basis the number cladocerans is lower in these lagoons and in Australian sites in general (Mitchell, 1986, Timms, 1970a). In that cladoceran assemblages are less rich in the study lagoons which are intermittently present, perhaps the ephemeral status of many Australian sites contributes to this Australia versus World difference. The explanation for this lies in the distinct seasonality of most cladocerans and hence greater likelihood of their absence from sites which dry intermittently. This also promotes erratic variation in species richness among cladocerans whereas among calanoids community structure is more stable (Table 2). Further study on this factor as well as others mentioned by Mitchell (1986) is needed.

A further method of comparing assemblages is by calculating the average percentage composition of the component species from regular samples taken over at least a year. This is done in Table 1 and has already been used (see above) to highlight similarities and differences between lagoons. Also of interest is the relative overall contribution by cladocerans (42%), calanoids (42%) and cyclopoids (16%) (Table 1). These proportions are not dissimilar from those (36 : 49 : 15 respectively) for Australian lakes reviewed by Mitchell (1986) and provide further evidence for the relatively greater contribution by calanoids in Australia *vis-à-vis* most other countries. Possible reasons for this are partly explored by Mitchell (1986), to which perhaps should be added the apparently great

TABLE 2

Average Momentary Species Composition in the Lagoons

Lagoon	Month												Grand Mean
	J	F	M	A	M	J	J	A	S	O	N	D	
	Calanoida												
1a	1.8	1.8	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.97
1b	2.0	1.6	1.6	1.6	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.87
2	—	1.5	1.0	1.7	1.7	1.7	1.7	1.5	1.5	1.7	2.0	1.5	1.59
3	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.00
4	2.0	1.5	1.5	1.5	2.0	2.0	2.0	2.0	2.0	2.0	1.8	2.0	1.86
5	2.0	0.0	1.0	1.3	2.0	2.0	2.0	2.0	2.0	2.0	1.7	2.0	1.67
All	1.9	1.4	1.5	1.8	1.9	1.9	1.9	1.9	1.9	1.9	1.9	1.9	1.83
	Cyclopoida												
1a	2.0	1.8	2.0	1.8	1.4	1.2	1.2	1.4	1.2	1.6	1.5	1.5	1.55
1b	2.0	2.0	1.8	1.4	1.4	1.8	1.6	1.2	1.0	1.0	1.6	1.8	1.55
2	—	1.0	1.3	1.7	1.7	1.0	1.3	1.0	1.5	1.3	2.0	2.0	1.44
3	1.3	1.3	1.3	1.3	1.0	1.5	1.5	1.0	1.5	1.3	1.0	1.0	1.21
4	1.3	1.3	0.5	1.0	1.3	1.3	1.3	1.3	1.7	1.3	1.3	2.0	1.30
5	2.0	0.5	1.5	1.0	1.0	1.0	1.0	1.7	2.0	0.7	1.0	2.0	1.28
All	1.7	1.3	1.2	1.4	1.3	1.3	1.3	1.3	1.5	1.2	1.4	1.7	1.39
	Cladocera												
1a	3.2	3.6	3.8	3.2	3.4	3.2	3.2	2.8	2.4	3.0	4.0	3.2	3.25
1b	4.0	3.6	3.8	4.8	4.0	3.2	2.6	3.6	4.0	4.2	4.3	3.4	3.83
2	—	2.5	3.0	2.0	3.3	1.7	1.7	1.5	2.5	3.0	3.0	2.5	2.43
3	3.3	2.3	2.5	2.5	2.8	3.0	3.0	3.0	2.7	4.0	3.3	2.3	2.89
4	2.3	2.0	2.0	2.0	3.0	2.0	2.0	2.0	2.5	3.2	3.5	2.7	2.43
5	0.0	2.0	1.0	2.0	2.0	2.0	2.0	2.3	2.3	2.0	3.0	2.0	1.88
All	2.6	2.7	2.7	2.8	3.1	2.5	2.4	2.5	2.7	3.2	3.6	2.7	2.79

adaptability and comparatively good dispersal powers of many centropagid copepods in Australia (Bayly, 1964, Maly, 1984a, Timms, 1970a, 1987a).

(d) **Recovery from Dryness**

The succession of species following refilling is broadly similar to that seen in the colonization of an entirely new waterbody (Timms, 1987a). *Moina micrura* and cyclopoids are fast colonizers, followed by *Boeckella fluvialis* and *Daphnia carinata*, then *Bosmina meridionalis* and finally, *Calamoecia lucasi* and *Daphnia lumholtzi*. The exact sequence in any succession is influenced by season. In the present lagoons, if the February and April recoveries are compared, *Daphnia carinata* did better and *Moina micrura* worse in April in accordance with their usual importance in these months (Figs 1 and 2). Also for similar reasons, *Diaphanosoma excisum* did well in one February recovery and *Bosmina meridionalis* in one April recovery. Generally cyclopoids and cladocerans responded quicker to refilling than calanoids, which is explained by the shorter life cycles of the former (Hutchinson, 1967). Of the calanoids, *Boeckella fluvialis* typically responded quicker than *Calamoecia lucasi* to refilling, as it produces more eggs and hence more offspring (Maly, 1984a).

There are two significant differences between the colonization of a new waterbody and recovery in a refilled one. The first is the absence of *Boeckella minuta*, a prime colonizer of new habitats (Bayly, 1979; Maly, 1984a; Timms, 1970a, 1987a). Perhaps it did arrive during recovery (and at other times as well) but was reproductively swamped or competitively excluded by the incumbent *Boeckella fluvialis* (Maly, 1984b). Similar reasons probably account for the failure of *B. triarticulata* to establish in Lagoon 5. The other difference is the greater rapidity of succession in lagoons recovering from dryness. This could be caused by the greater numbers of resting eggs (and hence nauplii hatching) in the recovery lagoon compared with the presumed few dissemules arriving at a new waterbody.

ACKNOWLEDGEMENTS

I wish to thank Dr Patrick De Deckker for identifying ostracods, Dave Morton for identifying cyclopoids , and Dr Ian Bayly and Dr Rus Shiels for their comments on the manuscript.

References

BAYLY, I. A. E., 1961. — A revision of the inland water genus *Calamoecia* (Copepoda: Calanoida). *Aust. J. Mar. Freshw. Res.* 12: 54-91.

—— 1964. — A revision of the Australian species of the freshwater genera *Boeckella* and *Hemiboeckella* (Copepoda: Calanoida). *Aust. J. Mar. Freshw. Res.* 15: 180-238.

—— 1966. — The Australian species of *Diaptomus* (Copepoda: Calanoida) and their distribution. *Aust. J. Mar. Fresh. Res.* 17: 123-134.

—— 1979. — Further contributions to knowledge of the Centropagid genera *Boeckella*, *Hemiboeckella* and *Calamoecia* (Athalassic calanoid copepods). *Aust. J. Mar. Freshw. Res.* 30: 103-127.

—— and MORTON, D. W., 1978. — Aspects of the zoogeography of Australian microcrustaceans. *Verh. Int. Ver. Limnol.* 20: 2537-2540.

BOTTRELL, J., *et al.*, 1976. — A review of some problems in zooplankton production studies. *Norw. J. Zool.* 24: 419-456.

GEDDES, M. C., 1968. — Studies on the Marshall Reserve pond with special reference to *Boeckella triarticulata* Thompson (Copepoda: Calanoida). Clayton, Victoria: Monash University, honours thesis unpubl.

—— 1984. — Seasonal studies on the zooplankton community of Lake Alexandrina, River Murray, South Australia, and the role of turbidity in determining community structure. *Aust. J. Mar. Freshw. Res.* 35: 417-426.

—— 1986. — Understanding zooplankton communities in farm dams: the importance of predation. *In* DE DECKKER, P., and WILLIAMS, W. D., (eds), *Limnology in Australia*: 387-401. Melbourne/Dordrecht: CSIRO/Junk.

GRANT, J. W. G., and BAYLY, I. A. E., 1981. — Predator induction of crests in morphs of the *Daphnia carinata* King complex. *Limnol. Oceanogr.* 26: 201-218.

HUME, D. J., FLETCHER, A. R., and MORISON, A. K. 1983. — Final Report. Carp Program. Arthur Rylah Inst. for Environ. Res., Fish. and Wildl. Div., Min. Cons., Victoria. 213 pp.

HUTCHINSON, G. E., 1967. — *Treatise on Limnology. Vol. II. Introduction to Lake Biology and the Limnoplankton.* New York: John Wiley and Sons.

JOLLY, V. H., 1966. — The limnetic crustacea of six reservoirs in the Sydney area of New South Wales. *Verh. Int. Ver. Limnol.* 16: 727-734.

LLOYD, L. N., ARTHINGTON, A. H., and MILTON, D. A. 1986. — The mosquitofish — a valuable mosquito-control agent or a pest? *In* KITCHING, R. J., (ed.), *The Ecology of Exotic Animals and Plants in Australia:* 7-25. Brisbane: John Wiley and Sons.

MALY, E. J., 1984a. — Dispersal ability and relative abundance of *Boeckella* and *Calamoecia* (Copepoda: Calanoida) in Australian and New Zealand waters. *Oecologia (Berl.)* 62: 173-181.

—— 1984b. — Interspecific copulation in and co-occurrence of similar-sized freshwater centropagid copepods. *Aust. J. Mar. Freshw. Res.* 35: 153-165.

MITCHELL, B. D., 1986. — Entomostracan zooplankton communities of Australian freshwater lakes and ponds. *In* DE DECKKER, P., and WILLIAMS, W. D., (eds), *Limnology in Australia*: 369-386. Melbourne/Dordrecht: CSIRO/Junk.

MORTON, D. W., 1985. — Revision of the Australian Cyclopoidae (Copepoda: Cyclopoida) I. *Acanthocyclops* Kiefer, *Diacyclops* Kiefer and *Australocyclops* gen. nov. *Aust. J. Mar. Freshwat. Res.* 36: 615-634.

PENNAK, R. W., 1949. — Annual limnological cycles in some Colorado reservoir lakes. *Ecol. Monogr.* 19: 233-267.

—— 1957. — Species composition of limnetic zooplankton communities. *Limnol. Oceanogr.* 2: 222-232.

REYNOLDS, J. G., and GEDDES, M. C., 1984. — Functional response analysis of size-selective predation by the notonectid predator *Anisops deanei* (Brooks) on *Daphnia thomsoni* (Sars). *Aust. J. Mar. Freshw. Res.* 35: 725-733.

SHIEL, R. J., WALKER, K. F., and WILLIAMS, W. D., 1982. — Plankton of the lower Murray River, South Australia. *Aust. J. Mar. Fresh. Res.* 33: 301-327.

SMIRNOV, N. N., and TIMMS, B. V., 1983. — A revision of the Australian Cladocera (Crustacea). *Rec. Aust. Mus., Suppl.* 1: 1-132.

STRASKRABA, M., 1965. — The effect of fish on the number of invertebrates in ponds and streams. *Mitt. Int. Verein. Limnol.* 13: 106-127.

TIMMS, B. V., 1967. — Ecological studies on the Entomostraca of a Queensland pond with special reference to *Boeckella minuta* Sars (Copepoda: Calanoida). *Proc. Roy. Soc. Qd* 79: 41-70.

—— 1970a. — Chemical and zooplankton studies on lentic habitats of north-eastern New South Wales. *Aust. J. Mar. Freshw. Res.* 21: 11-33.

—— 1970b. — Aspects of the limnology of five small reservoirs in New South Wales. *Proc. Linn. Soc. N.S.W.* 95: 46-59.

—— 1973. — A limnological survey of the freshwater coastal lakes of east Gippsland, Victoria. *Aust. J. Mar. Freshw. Res.* 24: 1-20.

—— 1987a. — Colonization of two large farm dams on the central coast of New South Wales by crustacean zooplankton. *Bull. Aust. Soc. Limnol.* 11: 9-14.

—— 1987b. — Geomorphic and physicochemical features of floodplain waterbodies of the lower Hunter Valley, N.S.W. *Proc. Linn. Soc. N.S.W.* 109: 311-324.

—— and MORTON, D. W., 1988. — Crustacean zooplankton assemblages in freshwaters of tropical Australia. *Hydrobiologia* 164: 161-169.

WALKER, K. F., and HILLMAN, T. J., 1977. — Limnological survey of the River Murray in relation to Albury-Wodonga, 1973-1976. Report on behalf of Gutteridge, Haskins & Davey to the Albury-Wodonga Development Corporation, Albury.

Seed Type and Seed Surface Patterns in *Calandrinia* sens. lat. (Portulacaceae)

SYEDA SALEHA TAHIR and ROGER CAROLIN

SYEDA SALEHA TAHIR, & CAROLIN, ROGER, Seed type and seed surface patterns in *Calandrinia* sens. lat. (Portulacaceae). *Proc. Linn. Soc. N.S.W.* 110 (4), (1988) 1989: 307-316.

Seed types of *Calandrinia* are defined as six shapes which are determined by the shape of the embryo and the amount of perisperm present. Ten surface patterns are described and the presence or absence of an aril are considered. The species usually have characteristic shapes and surface patterns but these features rarely characterize the segregate genera or the sections. Within some of the segregate genera and sections, however, there appear to be definite, and sometimes characteristic, phylogenetic trends in these features.

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INTRODUCTION

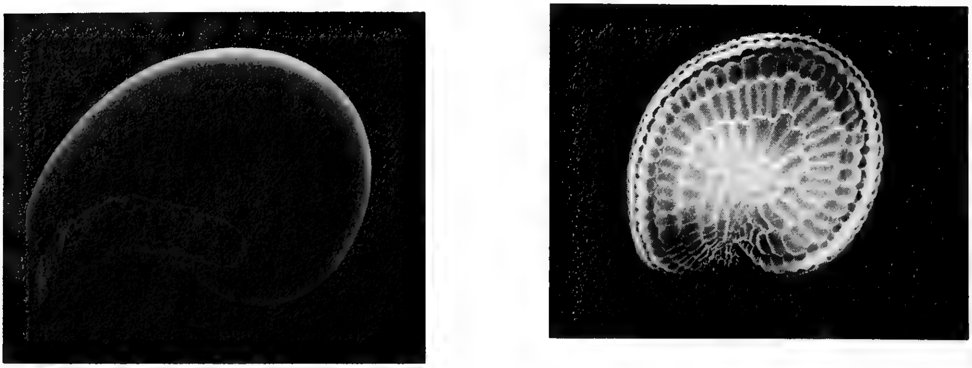
Seed type and seed surface pattern have been used extensively in plant taxonomy. Carolin (1987) has shown that the former, in particular, is useful at the generic level in the family Portulacaceae and has indicated that in certain genera, surface pattern can be useful in distinguishing between species (see also Cullen, 1953). Furthermore, the aril or strophiole, in this case derived from the funicle, has been used in the past to discriminate between genera, e.g., Pax and Hoffman (1935). This investigation seeks to establish the use of these features for the taxonomy within the genus *Calandrinia.*

The genus *Calandrinia* consists of about 130 species of which about 50 occur in Australia. Carolin (1987) has suggested that the genus be divided into five genera, *Calandrinia* sens. strict., *Cistanthe*, *Baitaria*, *Schreiteria* and *Rumicastrum.* The necessary combinations have not been made, except in *Schreiteria,* and here they will all be referred to as *Calandrinia* with the segregate name in parentheses. Although seed surface pattern has been used in the past to distinguish between some Australian species, e.g., Black (1948) and Reiche (1888), the only general survey of either seed type or surface pattern in these species is that of Syeda (1980). This contribution details the variation in these characters, provides a terminology and suggests a phylogeny for these characters.

MATERIAL AND METHODS

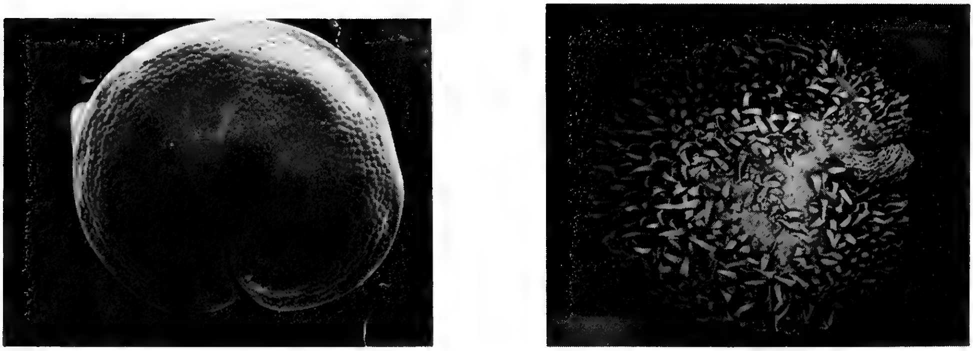
The mature seeds were taken from herbarium specimens and mounted on a stub with double sided sticky tape. They were then coated with 200-400 Å thickness of gold in a polaron coating machine and examined with a JSM-U3 scanning electron microscope. Two to three samples from different collections were examined for 77 species in this manner but in most cases only one voucher is listed here (Table 1). Where available, the seeds of most specimens of each species were examined using a stereo-microscope to check for variation within a species.

Hand sections were cut to ascertain the shape of the embryo and the distribution of the perisperm.



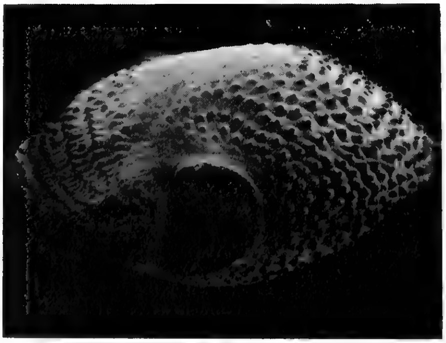
A. C. strophiolata

B. C. polyandra



C. C. tenuifolia

D. C. grandiflora



E. C. compressa

Fig. 1. **A.** *C. strophiolata*; **B.** *C. polyandra*; **C.** *C. tenuifolia*; **D.** *C. grandiflora*; **E.** *C. compressa*. (Bars indicate 100μ).

RESULTS

SEED SHAPES

The seed shape presented some problem since the differences between species, though often clear, are relatively slight and difficult to describe in words. The shapes defined in the chart of plane shapes reproduced in Stearn (1966) are not entirely satisfactory for 3-dimensional objects. Nevertheless, many workers do use them in this context, usually apparently referring to the projected shadow across the long axis. The shapes of *Calandrinia* seeds, however, do not always correspond to the standards even when thus projected onto a plane. Stearn also provides a chart of spore shapes from Ainsworth and Bisby; where these terms apply we have used them. Moreover some of the shapes integrade with each other and the decision as to their classification in some cases is a little arbitrary. The terms are redefined below in this particular context and illustrated in Figs 1 and 2.

Seed shape is a function of the shape of the embryo and, to a lesser extent, the amount of perisperm. The curvature and length of the embryo, and the relative growth of the radicle in relation to the cotyledons, determine the position of the funicle. The schematic diagrams in Fig. 3 illustrate this:

Oblong/Orbicular: Embryo almost completely encircling the perisperm; funicle attachment symmetrical at the base; ± compressed. The two shapes intergrade closely, e.g. *C. oblonga* (Fig. 2**F**). See Fig. 3**A**, **B**.

Notched Oblong/Orbicular: As for oblong but growth of both radicle and cotyledons continued below the funicular attachment, giving a basal notch, e.g. *C. tenuifolia* (Fig. 1**C**), *C. polyandra* (Fig. 1**B**). See Fig. 3**C**.

Obovoid to globular: Embryo almost encircling the perisperm but growth of the radicle continued below the funicular attachment thus causing the latter to be asymmetric; sometimes this distortion becomes extreme; not or very little compressed, e.g. *C. ptychosperma* (Fig. 2**C**), *C. reticulata* (Fig. 2**D**), *C. grandiflora* (Fig. 1**D**). See Fig. 3**D**.

Asymmetric clavate: Embryo not quite encircling the perisperm, funicle attached to one side of a basal point; not compressed, e.g. *C. lehmannii.*, This represents a type intermediate between obovoid/globular and curved.

Curved: Embryo not encircling perisperm but curved distally; funicle attached to one side of a basal point; not compressed, e.g. *C. primuliflora* (Fig. 2**E**). See Fig. 3**F**.

Narrow-obovoid: A very narrow seed but similar to the obovoid form described above; scarcely compressed, e.g. *C. disperma.*

There are, of course, intermediate states, some of which may indicate phylogenetic series.

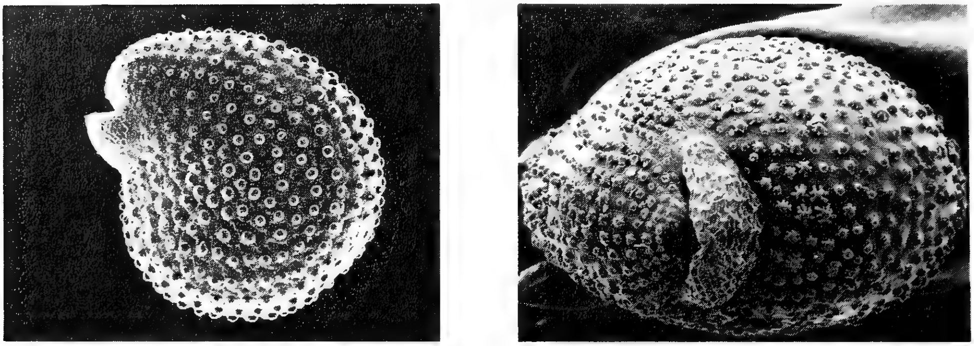
SEED SURFACE PATTERN

Here also the terms described by Stearn (1966) for surface patterns need some amendment as defined below:

Smooth: No prominent pattern, the outline of the epidermal cells usually visible but the surface between the radial walls flat, e.g. *C. strophiolata* (Fig. 1**A**).

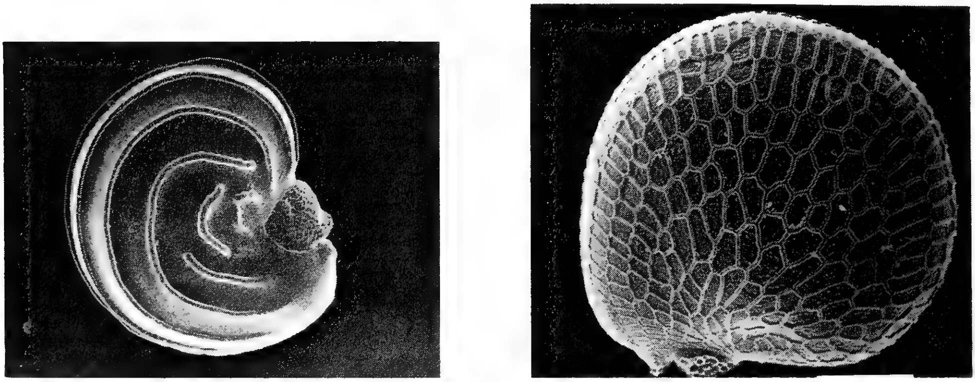
Colliculate: The surface of each epidermal cell is slightly raised into a shallow dome forming a closely packed pattern, e.g. *C. polyandra* (Fig. 1**B**).

Reticulate: The radial walls of each epidermal cell are raised into a ridge, e.g. *C. reticulata* (Fig. 2**D**).



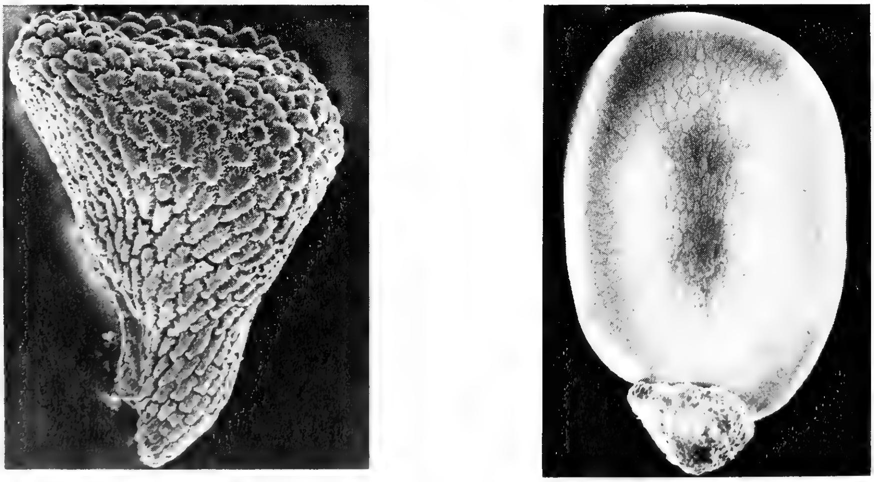
A. C. arenaria

B. C. pickeringii



C. C. ptychosperma

D. C. reticulata



E. C. primuliflora

F. C. oblonga

Fig. 2. **A.** *C. arenaria*; **B.** *C. pickeringii*; **C.** *C. ptychosperma*; **D.** *C. reticulata*; **E.** *C. primuliflora*; **F.** *C. oblonga*. (Bars indicate 100μ).

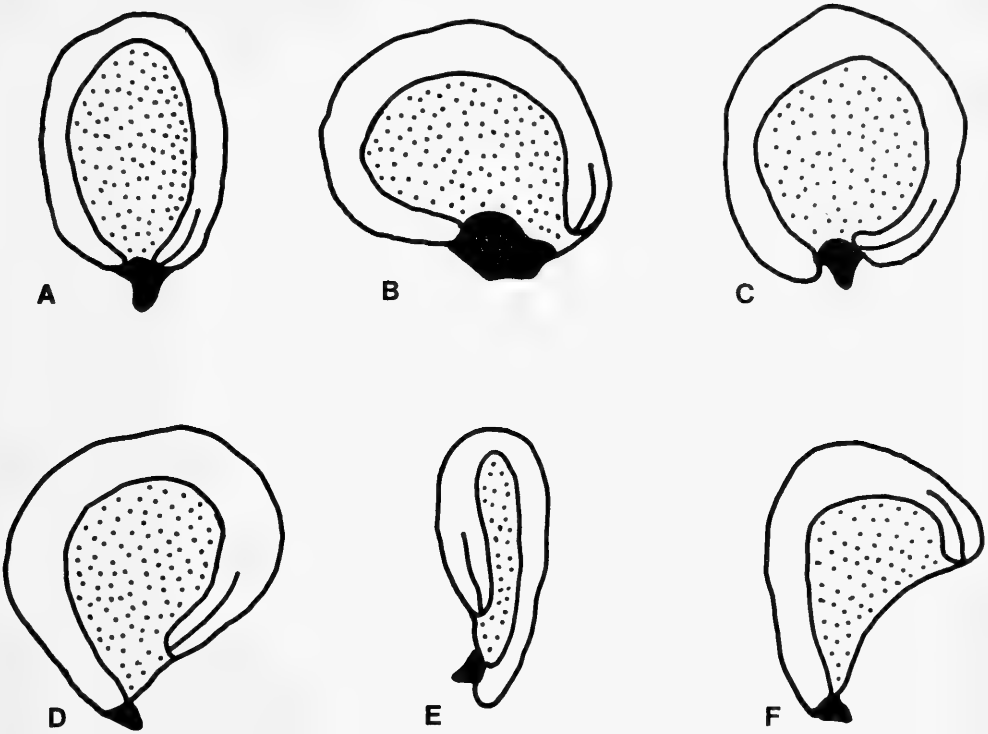


Fig. 3. Schematic diagrams to show seed shape and its associated features. **A.** Oblong/(orbicular); **B.** (Oblong)/orbicular: **C.** Notched oblong/orbicular; **D.** Obovoid; **E.** Narrow obovoid; **F.** Curved.

Papillate: The centre of the outer tangential wall of the epidermal cell is projected into a short rounded papilla e.g. *C. compressa* (Fig. 1**E**). Generally the cells of the epidermis tend to be aligned into rows and thus, so do the papillae. In some species this is more pronounced than in others and in this case the pattern may be referred to as aligned-papillate, e.g. *C. arenicola.*

Aculeate: Similar to tuberculate in which the papillae are extended into a long narrow hair-like process, e.g., *C. grandiflora* (Fig. 1**D**).

Polypiform: In this case the papillae have short lobes over their surface, e.g., *C. arenaria* (Fig. 2**A**).

Papillate-punctate: Similar to papillate but with a small pit at the corner junctions of each cell, e.g. *C. pickeringii* (Fig. 2**B**).

Ribbed: The surface is marked by prominent ribs which are the confluent papillae of adjacent aligned cells, e.g. *C. ptychosperma* (Fig. 2**C**).

Tuberculate: The papillae project into broad finger-like processes e.g. *C. lehmannii.*

Verrucate: Similar to tuberculate but the tubercles are somewhat shorter and, although the top is smooth, the sides are ridged as though they were thinner, thus giving a warty appearance, e.g. *C. primuliflora* (Fig. 2**E**).

ARIL

It is often difficult to determine whether an aril is present or not since small fragments of the funicle may be left on the seed due to the abscission occurring well below the insertion of the funicle on the seed. The fragment left may or may not function as an elaiosome in ant dispersal. It seems possible that a well developed aril is an elaiosome as in *C. grandiflora* (Carolin, pers. obs.). This true aril is the swollen upper part of the funicle and the primary abscission occurs below it; this is registered as '+' e.g. *C., ptychosperma* (Fig. 2**C**), *C. strophiolata* (Fig. 1**A**), *C. grandiflora* (Fig. 1**D**), *C. arenaria* (Fig. 2**A**). When only a slight swelling, or none at all, occurs above the primary abscission but a fragment of funicle remains on the seed this is registered as '±' e.g. *C. polyandra* (Fig. 1**B**). When the primary abscission occurs at the insertion of the funicle on the seed this is registered as '–' e.g. *C. tenuifolia* (Fig. 1**C**), *C. compressa* (Fig. 1**E**), *C. primuliflora* (Fig. 2**E**).

The results are summarized in Table 1, in which the Australian species are grouped according to the sections of Syeda (1980) and the others are grouped according to Carolin (1988).

TABLE 1

Species examined for seed characteristics in the course of this investigation

(Vouchers are given using the herbarium number where one is available. Where one is not available the herbarium is indicated and the collector and collector's number are given. Herbarium codes are taken from Index Herbariorum)

Species name	shape	pattern	aril	Voucher
Calandrinia (*Cistanthe*) sect. Cistanthe				
C. arenaria Cham.	obov	Sm/Co	+	CONC 47320
C. cachinalensis Phil.	obov	Po	+	NO VOUCHER
C. coquimbensis Barn.	obov	Ac	+	NO VOUCHER
C. frigida Barn.	obov	Pp	+	CONC 32814
C. glaucopurpurea Reiche	obov	Po	+	NO VOUCHER
C. grandiflora Lindl.	obov	Ac	+	Carolin 14022 SYD
C. litoralis Phil.	obov	Po	+	CONC 47322
C. longiscapa Barn.	obov	Po	+	NO VOUCHER
C. maritima Nutt.	obov	Ac	+	NO VOUCHER
C. oblongifolia Barn.	obov	Po	+	Carolin 14112 SYD
C. solisii Phil.	obov	Po	+	NO VOUCHER
C. thyrsoidea Reiche	obov	Ac	+	CONC 8396
Calandrinia (*Cistanthe*) sect. Amarantoideae				
C. ambigua Nutt.	obov	Pp	—	B 1417582
C. calycina Phil.	ob/or	Sm/Co	—	CONC 33144
C. spicigera Phil.	ob/or	Sm/Co	—	CONC 47320
Silvaea pachyphylla Phil.	ob/or	Sm/Co	—	CONC 9365
Calandrinia (*Baitaria*) sect. Dianthoideae				
C. andicola Gill. ex Arn.	n.ob/or	Sm	—	CONC 49244
C. cistiflora Gill.ex.Arn.	n.ob/or	Co	—	CONC 3200
C. gayana Barn.	n.ob/or	Co/Sm	—	CONC 4898
C. patagonica Speg.	ob/or	Co	—	CONC 34827
C. tenuifolia Phil.	n.ob/or	Co	—	CONC 32104
Calandrinia sens. strict.				
C. axilliflora Barn.	obov	Pp	±	CONC 49732
C. compressa Schrad.	obov	Pp/Co	±	Carolin 14000 SYD
C. ciliata (Ruiz & Pavon) DC.	obov	Co	±	Carolin 14090 SYD
Calandrinia (*Baitaria*) sect. Hirsutae Hook. & Arn.				
C. sericea Hook. & Arn.	obov	Co	—	Carolin 14121 SYD
C. umbellata (Ruiz & Pavon) DC.	obov	Sm	—	Boelcke 13859 SYD
C. uspalatensis Phil.	obov	Co	—	Carolin 14090 SYD

TABLE 1 (continued)

Species name	shape	pattern	aril	Voucher
Calandrinia (*Baitaria*) sect. Condensatae				
C. capitata Hook. & Arn.	ob/or	Sm	—	Carolin 14011 SYD
C. demissa Phil.	obov	Pp	—	CONC 8568
C. floribunda Phil.	obov	Co	—	Carolin 14109 SYD
C. glomerata Phil.	ob/or	Co	—	CONC 41891
C. leucocephala Phil.	ob/or	Co	—	Carolin 14108 SYD
C. modesta Phil.	obov	Co	—	CONC 32801
C. polycarpoides Phil.	obov	Co	—	CONC 32732
C. prostrata Phil.	obov	Co	—	CONC 32747
C. trifida Hook. & Arn.	ob/or	Co/Sm	—	Carolin 14024 SYD
Calandrinia (*Baitaria*) sect. Acaules				
C. acaulis (Ruiz & Pavon) HBK.	obov	Pp	±	LIL 408812
C. affinis Gill. ex Arn.	obov	Sm/Co	±	Carolin 14013 SYD
C. affinis Gill. ex. Arn.	obov	Pp	±	Carolin 14014 SYD
C. caespitosa Gill. ex Arn.	obov	Co/Sm	—	Carolin 14122 SYD
C. fuegiana Gand.	obov	Co	—	CONC 32743
C. megarrhiza Helmsl.	obov	Co	—	RSA 631344
Calandrinia (*Rumicastrum*) sect. Pseudodianthoideae				
C. arenicola Syeda	n.ob/or	Ap	+	TYPE BRI 108559
C. balonensis Lindl.	n.ob/or	Co	±	AD 96923308
C. brevipedata F. Muell.	ob/or	Sm	±	TYPE MEL 48539
C. calyptrata Hook. f.	ob/or	Sm	±	AD 97314277
C. composita (Nees) Benth.	n.ob/or	Co	±	TYPE MEL 48615
C. corrigioloides F. Muell. ex Benth.	ob/or	Sm	±	TYPE MEL 48628
C. creethiae Morrison	obov	Sm-Co	±	C. A. Gardner 7821 PERTH
C. disperma J. M. Black	nr. obov (see text)	Co-Pp	—	P. G. Wilson 8414 PERTH
C. eremaea Ewart	n.ob/or	Pp	±	AD 96913076
C. granulifera Benth.	obov	Co	±	AD 96929529
C. liniflora Fenzl	ob/or	Sm	±	H. Demarz 2725 PERTH
C. monosperma Syeda	obov	Sm	—	TYPE PERTH
C. pickeringii Gray	obov	Pp-p	±	BRI 015191
C. pleiopetala F. Muell.	obov	Co	±	TYPE MEL 48743
C. polyandra Benth.	n.ob/or	Co	±	AD 96343036
C. pumila F. Muell.	obov	Sm-Co	+	TYPE MEL 48789
C. quadrivalvis F. Muell.	obov	Co	±	TYPE MEL 48799
C. remota J. M. Black	ob/or	Sm	P	AD 96416002
C. reticulata Syeda	obov	Rt	P	TYPE NT 43058
C. sphaerophylla J. M. Black	n.ob/or	Co	±	TYPE AD 97826032
C. stagnensis J. M. Black	obov	Sm-Co	±	TYPE AD 96846192
C. strophiolata F. Muell.	obov	Sm	+	TYPE MEL 48826
C. volubilis Benth.	n.ob/or	Pp	±	TYPE MEL 48860
Calandrinia (*Rumicastrum*) sect. Tuberosae				
C. lehmannii Endl.	as-c	Tb	—	T. L. Setter 427 PERTH
C. primuliflora Diels	cu	V	—	MEL 48774
C. schistorrhiza Morrison	cu	Tb	—	T. E. H. Aplin 2434 PERTH
Calandrinia (*Rumicastrum*) sect. Basales				
C. gracilis Benth.	obov	Co	±	BRI 053297
C. papillata Syeda	n.ob/or	Pp	±	TYPE PERTH
C. pleiopetala F. Muell.	obov	Co	±	TYPE MEL 48743
C. porifera Syeda	obov	Co	±	TYPE PERTH

TABLE 1 (concluded)

Species name	shape	pattern	aril	Voucher
C. ptychosperma F. Muell.	obov	Rb	+	W. E. Mulham W941 NSW
C. spergularina F. Muell.	obov	Co	±	TYPE MEL 48819
C. uniflora F. Muell.	ob/or	Sm	—	AD 96919061
Schreiteria				
S. macrocarpa (Speg.) Carolin	oblong	Co/pap	—	LIL Schreiter 4857

Abbreviations used for seed shapes:
as-cl = asymmetric-clavate; cu = curved; n.ob/or = oblong to orbicular with a notch at insertion of funicle; ob/or = oblong to orbicular, ± symmetric at base; obov = obovoid, ± asymmetric at base; nr. obov = narrow obovoid.

Abbreviations used for surface patterns:
Ac = aculeate; Ap = aligned papillate; Co = colliculate; Po = polypiform; Pp = papillate; Pp-p = papillate-punctate; Rb = ribbed; Rt = reticulate; Sm = smooth; Tb = tuberculate; V = verrucate. *Schreiteria* is coded differently to indicate that the surface and shapes here are not comparable with the others in the table.

DISCUSSION

This survey indicates that there is range of seed types and seed surface patterns in *Calandrinia* sens. lat., and that they have a significant role to play in species recognition.

Whilst the transformation series of seed shape and surface pattern are fairly clear, the polarization of these states, in the latter case at least, is not clear. The cladogram presented by Carolin (1987) indicates that the outgroup of the clade containing all of the segregate genera except *Schreiteria* is the *Portulaca* group of genera. This outgroup is equivocal for these characters. The outgroup of the whole family is Aizoaceae and little is published about the seed shape and surface patterns of this group.

Shape

There seems little doubt that curved shapes and those containing reduced endosperm are advanced features since they do not seem to occur in the Aizoaceae. The curved shape, together with the curved embryo and reduced perisperm, also occurs in the *Portulaca* group of genera (Carolin, 1987). The occurrence in the *Portulaca* group is considered to be a separate origin of the feature.

We suggest that the oblong/orbicular and notched-oblong/orbicular shapes may represent the primitive condition whilst obovoid represents an asymmetry of the embryo at the base of the seed; the asymmetric-clavate and curved shapes represent an increasing asymmetry of the embryo. The narrow-obovoid shape is a special case found together with a narrow clavate shape in the heterospermic species, *C. disperma*, whilst *Schreiteria macrocarpa*, has an oblong seed with a reduced perisperm thus making the seed much narrower than the other oblong types. These are derivative forms of the obovoid or oblong shapes and are not equivalent to the curved type with reduced perisperm, since the embryo still almost encircles the perisperm.

Seed surface pattern

The cladogram presented by Carolin (1987) is equivocal with regard to the primitive state of seed surface pattern. Both papillate and smooth patterns occur in *Calandrinia* (*Baitaria*) and evidence is lacking for Aizoaceae. Although it might seem more likely that the smooth condition is more primitive from a morphogenetic point of view, the evidence is slim. For the purposes of this description the smooth pattern is taken as a starting point but some amendment of this will probably be necessary as more characters of this group are considered.

The colliculate pattern is a derivation of smooth by the development of the surface into a dome. Papillate represents an upgrowth from this dome with aculeate, tuberculate and polypiform as further developments of that upgrowth. The papillate-punctate is a development from the papillate type as indicated above. The ribbed pattern is a development from the aligned papillate pattern as indicated above. The reticulate pattern is a quite separate development from colliculate/smooth patterns. Fig. 4 illustrates the putative evolutionary sequence in this character.

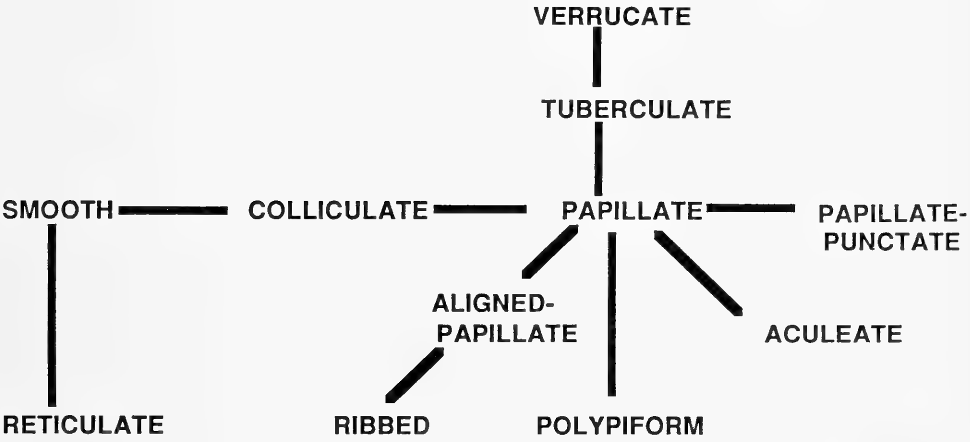


Fig. 4. The suggested transformation series of seed surface pattern.

Aril

It is equally difficult to conclude whether the presence or absence of an aril is primitive since the outgroups of both the family (see Corner, 1976) and the clade containing *Calandrinia* sens. lat. (Carolin, 1987), have arillate as well as exarillate seeds. It is probable that the aril is a response to particular dispersal requirements and if this is so the lack of it is likely to be primitive.

The segregate genera of *Calandrinia* sens. lat. are consistent neither in seed shape nor surface pattern and neither of these attributes thoroughly characterizes them. *Schreiteria* is monotypic with a more or less unique seed type having a very curved embryo with very little perisperm and a mostly colliculate surface with a few blunt papillae.

Calandrinia (*Baitaria*) consists mostly of species with colliculate or smooth surface patterns. Indeed, all those examined in sects Dianthoideae and Hirsutae have one of these two closely related patterns. One species in sect. Condensatae and two in sect. Acaules have papillate seeds. In fact, *C. affinis* at Farellones east of Santiago in Chile shows both papillate and colliculate surfaces in the same population.

Calandrinia (*Cistanthe*) shows several surface types. Within sect. Cistanthe there is a definite trend from smooth/colliculate through papillate to aculeate and polypiform surface. Most of the species have one or other of the two most advanced states. This trend is not shown in any of the other segregate genera. Even sect. Amaranthoideae has only smooth-colliculate and papillate surfaces. *Calandrinia* sens. strict. shows both papillate and colliculate surfaces.

Within *Calandrinia* (*Rumicastrum*) it is doubtful if the sections of von Poellnitz (1934) are natural. Syeda (1980) has suggested that there are only three recognizable sections within *Calandrinia* in Australia but this also may be open to question. The only section which is more or less consistent is sect. Tuberosae with a straighter embryo, less perisperm and a tuberculate or verrucate surface. Otherwise there would seem to be considerable homoplasy in these transformation series.

The aril may be of more use at the sectional level. All the species of *Calandrinia* (*Cistanthe*) sect. Cistanthe examined so far have arils. Likewise *Calandrinia* (*Cistanthe*) sect. Amaranthoideae, *Calandrinia* (*Baitaria*) sects. Dianthoideae, Hirsutae and Condensatae and *Schreiteria* do not have arils. The other taxa either have both conditions and/or have the indeterminate condition. It is clear, however, that one of the key characters provided by Pax and Hoffman (1935) to separate *Talinum* and *Calandrinia* (sens. lat.), viz., the presence or absence of an aril, is not satisfactory.

It seems, then, that the seed features are of limited value in distinguishing the segregate genera, although some genera and sections show distinct trends which, in the cases of *Calandrinia* (*Cistanthe*) and *Calandrinia* (*Rumicastrum*) sect. Tuberosae, are not repeated in other taxa at the same level. *C. pickeringii* and *C. reticulata* have unique surface patterns. The shape of the seed is also inconsistent within the segregate genera and sections except for *Calandrinia* (*Rumicastrum*) sect. Tuberosae, *Calandrinia* (*Cistanthe*) sect. Cistanthe and *Calandrinia* (*Baitaria*) sect. Acaules. *Schreiteria* occupies an isolated position within *Calandrinia* sens. lat. Indeed Carolin (1987) has suggested it is more closely related to the *Talinum* group of genera although the seed characters neither confirm nor contradict this.

It is clear from these results that the most variable of the segregate genera, with regard to seed shape and surface pattern, is *Calandrinia* (*Rumicastrum*). This greater variability is also shown in other characters such as fruit type and form of inflorescence.

ACKNOWLEDGEMENTS

We thank the Directors of the various Herbaria in Australia, Chile, Argentina, and U.S.A. who have lent material to us for this study from which seed samples have been taken. We thank also members of Universidad de Chile; Universidad de Concepcion; CEFAPRIN, Buenos Aires; Instituto Darwinion; Universidad de Cordoba and Instituto Lilloa for their help whilst RCC was engaged in collecting material for this study. In addition, we thank the staff of the Electron Microscope Unit at Sydney University for the use of their facilities, Tahir Rajput, Surrey Jacobs and Judy West for discussions on the work and Belinda Pellow and Cathy Miller for technical assistance. The University of Sydney provided funds which assisted in the investigation.

References

Black, J. M., 1948., — *Flora of South Australia*, ed. 2., vol. 2. Adelaide: Government Printer.

Carolin, R. C., 1987. — A review of the family Portulacaceae. *Austr. J. Bot.* 38: 383-412.

——, 1988. — Portulacaceae. *In* K. Kubitzki, (ed.), *Families and Genera of Flowering Plants*. In press.

Corner, E. J. H., 1976. — *The Seeds of Dicotyledons*, 2 vols. Cambridge: Cambridge University Press.

Cullen, D. C. Anon Suarez de, 1953. — Las especies argentinas del genero *Calandrinia* (Portulacaceae). *Bol. Soc. Arg. Bot.* 5: 1-112.

Pax, F., and Hoffman, K., 1935. — Portulacaceae. *In* A. Engler and H. Harms, (eds), *Die naturlichen pflanzenfamilien*, ed. 2, 16c: 233-262. Leipzig: Engelmann.

Poellnitz, K. von., 1934. — Die Calandrinien-Arten Australiens. *Fedde Rep.* 35: 161-173.

Reiche, K., 1888. — *Flora de Chile*, vol. II. Santiago: Universidad de Chile.

Stearn. W. T., 1966 — *Botanical Latin*. London: Nelson & Sons.

Syeda. S. T., 1980 — The genus *Calandrinia* HBK. in Australia. Sydney: University of Sydney, M.Sc. thesis, unpubl.

A late Holocene Vegetation and Fire Record from Ku-ring-gai Chase National Park, New South Wales

P. G. KODELA and J. R. DODSON

KODELA, P. G., & DODSON, J. R. A late Holocene vegetation and fire record from Ku-ring-gai Chase National Park, New South Wales. *Proc. Linn. Soc. N.S.W.* 110 (4), (1988) 1989: 317-326.

Pollen and charcoal analyses of sediments from South Salvation Creek Swamp in Ku-ring-gai Chase National Park indicate that pollen influx has been dominated by local swamp species and dry sclerophyll heath and woodland taxa for the last 6000 radiocarbon years. Fire occurred throughout the record but charcoal and *Eucalyptus* pollen influx decreased over the last 1700 years. In an environment supporting dry sclerophyll vegetation fire appeared to play a constant role. The swamp surface was initially a sedgeland but was invaded by *Gleichenia* and woody shrubs around 2500 b.p. None of the vegetation changes could be ascribed directly to climatic shifts but the origin of the swamp itself may have been due to the postglacial rise in sea-level.

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INTRODUCTION

Ku-ring-gai Chase National Park encompasses 14,700ha of natural bushland 20km north of Sydney. A palynological investigation was undertaken on a peat swamp deposit on the southern arm of Salvation Creek on Lambert Peninsula (Fig. 1) to investigate vegetation change and possible vegetation-fire relationships during the mid to late Holocene. The elevation of the site (130m a.s.l.) assures that it has remained beyond any direct effects of sealevel change.

Ku-ring-gai Chase experiences a temperate coastal climate with a mean annual rainfall exceeding 1200mm. Mean maximum temperatures range from 26°C in January to 16°C in July whilst mean minima range from 17°C in January to 7°C in July. The prevailing winds are northeast to northwest in summer and southwest to southeast in winter (Bureau of Meteorology, 1979; Fitzpatrick and Armstrong, 1972; National Parks and Wildlife Service, 1982).

The rugged topography of Ku-ring-gai Chase is strongly influenced by the predominant rock type, Hawkesbury Sandstone. Shales and sandstones of the underlying Narrabeen Group outcrop along the foreshores of the Hawkesbury River. Lambert Peninsula is characterized by deeply dissected V-shaped valleys with narrow divides on the west and extensive areas of low slope on the plateau surface and steep coastal gullies on the east (Buchanan, 1975, 1980). Pittwater forms part of the drowned river valley of the lower Hawkesbury River.

The study site, South Salvation Creek Swamp, has developed in a broad shallow valley on the gently sloping plateau. Drainage has been impeded by massive quartz sandstone and clayey layers derived from shale lenses within the Hawkesbury Sandstone group. Lamy and Junor (1965a) described the importance of such swamps in maintaining a perennial flow to creeks, reducing flood flows on the lower sections, controlling erosion, and arresting sedimentation.

Soils derived from siliceous Hawkesbury Sandstone tend to be light-coloured sandy loams with low humus content, poor water-retaining properties and low fertility

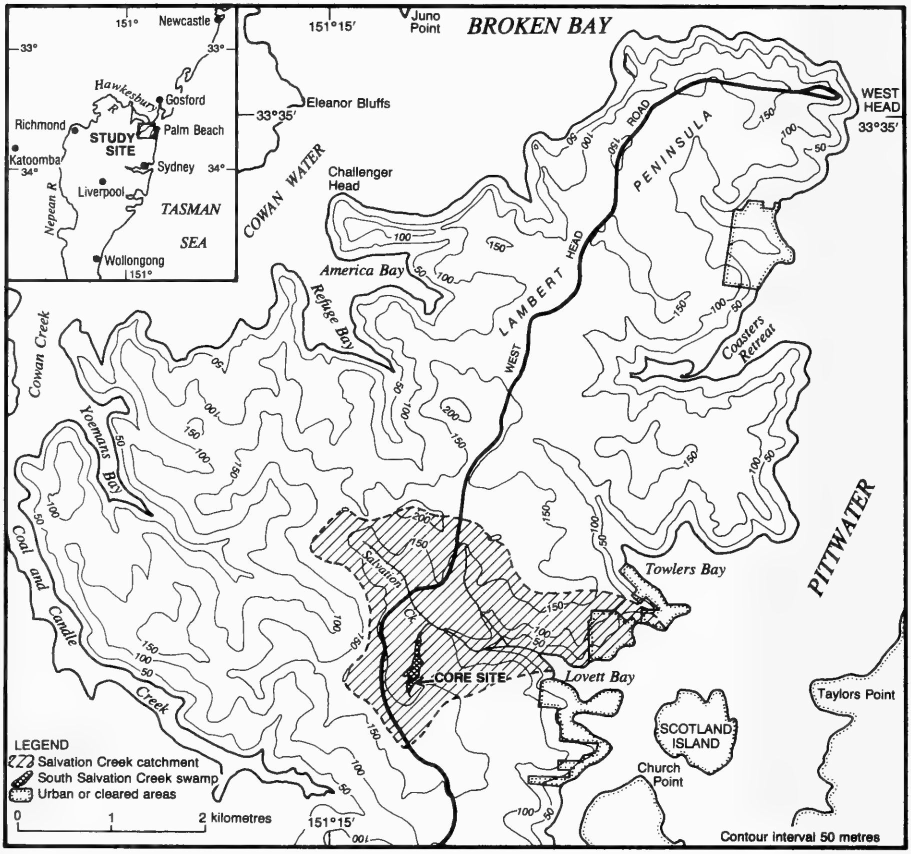

Fig. 1. Location of South Salvation Creek Swamp showing core location.

(Pidgeon, 1937; Lamy and Junor, 1965a, 1965b). On steep slopes and rocky outcrops sandy skeletal soils (lithosols) occur while deeper soils with some degree of profile development (towards yellow podzolics) are associated with the more gentle plateau slopes and hillslopes. Fine-textured loams of relatively higher-nutrient status, water-retaining capacity and humus content have developed on the Narrabeen shales.

The nature and distribution of the vegetation are strongly influenced by geology, topography, soil, drainage, aspect and fire (Buchanan, 1975, 1980; Kodela, 1984; Outhred *et al.*, 1985; Thomas and Benson, 1985). The dissected terrain and changes in lithology result in a complex mosaic of habitats and thus plant communities vary markedly in structure and floristics. The Salvation Creek catchment is dominated by woodland and heath on the exposed plateau surface and upper hillslopes while taller more mesic forests are confined to the sheltered lower slopes and gullies fronting Pittwater.

Descriptions are based on Thomas and Benson (1985) for terrestrial communities and Buchanan (1980) and Kodela (1984) for other types. Closed-scrub and heath occur in poorly-drained areas on the plateau, and shallow sandy soils on rocky sandstone outcrops. Shrub species commonly associated with moist heath include *Banksia ericifolia*, *Allocasuarina distyla* and *Hakea teretifolia*. Occasionally *Eucalyptus haemastoma* and *Eucalyptus gummifera* occur as emergents. Low woodland and low open-woodland occur on the better drained lithosols and sandy clay loams on ridges, crests and low to moderately sloping benched hillslopes. Common tree species include *E. gummifera*, *E. haemastoma* and *E. oblonga* often with a diverse shrub layer characterized by species from the families Epacridaceae, Fabaceae, Myrtaceae, Proteaceae and Rutaceae. Sheltered slopes with south to southeast aspects support open-forest of *E. piperita* ssp. *piperita*, *Angophora costata* and *E. gummifera*. The deeper more fertile soils on the shale and colluvium-derived soils of the lower slopes support *Eucalyptus maculata*, *E. paniculata*, *Allocasuarina torulosa* and *Syncarpia glomulifera*. Sheltered coastal gullies may contain small pockets of rainforest with *Ceratopetalum apetalum*, *Tristaniopsis laurina*, *Acmena smithii*, *Livistona australis*, *Synoum glandulosum* and *Elaeocarpus reticulatus*. South Salvation Creek Swamp has a complex of four swamp vegetation types (Buchanan, 1980). The dense cover is essentially sedge, fern and shrub-dominated. Below the tall (2-3m) emergent *Leptospermum juniperinum* there is a layer of *Banksia robur*, *Aotus ericoides* and *Gahnia sieberiana*. The surface layer is dominated by *Empodisma minus*, *Gleichenia dicarpa* and *Drosera binata*. Other swamp and moist heath species, often peripheral to the swamp, include *Gymnoschoenus sphaerocephalus*, *Xyris operculata*, *Lepidosperma* sp., *Sprengelia incarnata*, *Hakea teretifolia* and *Banksia ericifolia*.

METHODS

A vertical core of peat was extracted from the deepest sediment section with a Russian (D-section) corer (Jowsey, 1966). Subsamples at about 10cm intervals were dispersed in warm hydroxide, treated with hydrofluoric acid and acetolysis fluid (9 acetic anhydride: 1 concentrated sulphuric acid) and dehydrated through an alcohol series before the residue was mounted in silicone oil. The technique is based on that described by Erdtman (1969), Faegri and Iversen (1975) and Moore and Webb (1978). A minimum of 200 pollen grains and spores was counted for each sample depth and pollen sums for the percentage diagrams are based on the total count. Five peat samples were radiocarbon-dated to provide dates for the age-depth curve in Fig. 2 and the time scale in Figs 3 and 4. Loss-on-ignition was used as an estimate of organic content, and, using the point count method of Clark (1982), microscopic charcoal particles were counted as an index of fire activity.

RESULTS AND DISCUSSION

Stratigraphy

The core was predominantly herbaceous peat overlying a pallid inorganic layer of sand and clay. Within the peat the degree of humicity increased with increasing depth, from course fibrous peat at the surface to well-humified organic matter at the base. The gradual transition suggests a series of decay. The sediment can be summarized as follows:

Depth (cm)	Description
0-20	dense surface mat of undecomposed plant remains (mainly *Empodisma* and *Gleichenia*):
20-40	mainly water and living roots. Gradual transition to:
40-110	brown fibrous peat (*Turfa herbacea*), pH 4.5-5. Gradual transition to:
110-240	homogeneous fine fibrous clayey peat with charcoal fragments and quartz sand scattered throughout or in thin layers; pronounced H_2S odour. Distinct granular charcoal layer at base of peat (230-240cm). Sharp transition to:
240+	grey light-medium sandy clay (*Grana/Argilla*). Bedrock was encountered at *ca* 285cm.

Age and Origin of Site

The organic sediment dates from between 5000 and 6000 b.p. and marks either a regional change to greater effective precipitation, probably as a result of higher post-glacial sealevel, or a local geomorphic event such as damming of a stream outlet to allow sedimentation to occur. There is no clear evidence of the latter however. Buchanan (1975, 1980) suggested that the swamps of the Sydney region may be representatives of a cycle of swamp build-up and destruction. She suggested that climatic changes appear to be responsible for the cycles; and even in the short term such fluctuations over decades can affect swamp boundaries. Very dry climatic conditions can crack the peat surface, enable fires to burn the sediments and promote erosion when followed by heavy rain. The charcoal layer at the base of the peat (i.e. peat-inorganic boundary) may be an indication of such a process; alternatively the charcoal may have been stored in the catchment until deposition and preservation began. Such substantial layers of charcoal at the base of other peat or clay deposits have been observed by several investigators (Clark and Colhoun, pers. comm.; Macphail, 1984; Dodson *et al.*, 1986) and may be due to flush of charcoal into the system once sediments are able to accumulate or indeed may be part of a changed environment which leads to sedimentation itself. On a smaller scale, possibly reflecting periods of drought and fire, scoured shallow depressions are common on the exposed Hawkesbury Sandstone plateau while other depressions are inhabited by mosses, herbs and small shrubs which build up soil and organic matter.

Due to the general lack of distinct layers within the peat radiocarbon dates were not related to stratigraphy. Fig. 2 shows a general increase in accumulation rates toward the present, due at least in part to compaction increasing with depth. It is from this curve that ages in the text are estimated.

Pollen and Charcoal Record

Fig. 3 shows abundance of pollen for individual taxa based on percentage of the total pollen sum for each sampled sediment depth; in Fig. 4 estimates of pollen influx are shown for the more abundant pollen types. In these diagrams the modern sample incorporates the uppermost 15cm of sediment. Samples at 40 and 45cm represent 5cm sample thicknesses, i.e. 40-45cm and 45-50cm respectively, while all other samples represent 1cm sample thicknesses at 10cm intervals. Influx values are not calculated for the surface or more minerogenic samples; and there are missing loss-on-ignition values at several depths. The Appendix shows likely genera and species represented by the pollen taxa on the diagrams.

Tree pollen was dominated by *Eucalyptus*, but the values for *Allocasuarina* and *Banksia* may also contain some representation from trees. The highest values for *Eucalyptus* occur prior to 1900 b.p. for both influx and percentage values.

Charcoal is present throughout the record with highest values for both influx and concentrations between about 1300 b.p. and 3000 b.p. Charcoal concentration shows a decline from about 500 b.p. There is no consistent small-scale correlation between *Eucalyptus* and charcoal but the highest values for both occur prior to 1900 b.p.

Dryland herbs are poorly represented. These include Asteraceae, *Gonocarpus*, Liliaceae, Poaceae and *Pteridium*. An increase in herb pollen influx after 2000 b.p. may represent disturbance as many species in this group are competitive when clearance occurs. Although some of the herb taxa show slightly higher abundance values corresponding to relatively high fire activity, as indicated by charcoal, in this part of the record there are no consistent associations.

The total pollen input into the site is dominated by swamp taxa such as *Gleichenia*, Cyperaceae and Restionaceae; and is therefore very local in nature. There is a general trend of increasing *Gleichenia* spores to the present while Cyperaceae may have

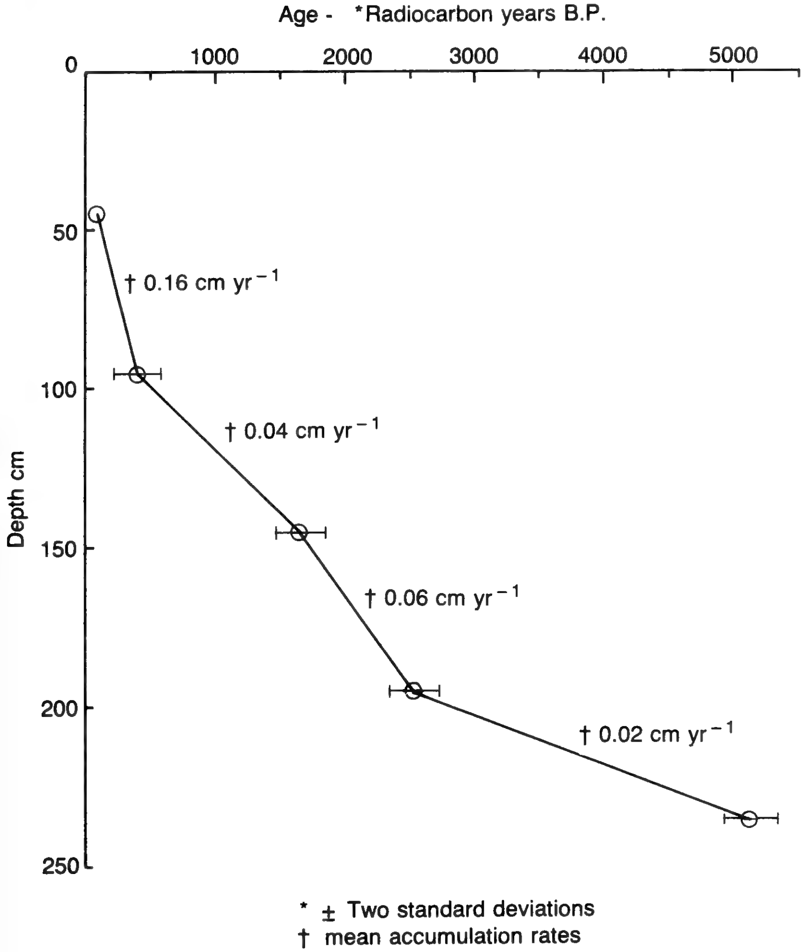

Fig. 2. Age-depth curve for the peat sediments.

decreased slightly. Restionaceae pollen increases markedly at 4900 b.p. where the peat layer overlies the inorganic sandy clay. Influx values for *Gleichenia*, Cyperaceae and Restionaceae appear somewhat cyclic, generally following changes in charcoal influx. Influx peaks for these taxa around 1700 b.p. and 500 b.p. correspond to peaks in charcoal and may indicate fires on or near the swamp promoting growth of these taxa.

Past Vegetation and Environmental History

There have been no marked changes in the flora; all the major pollen taxa remained

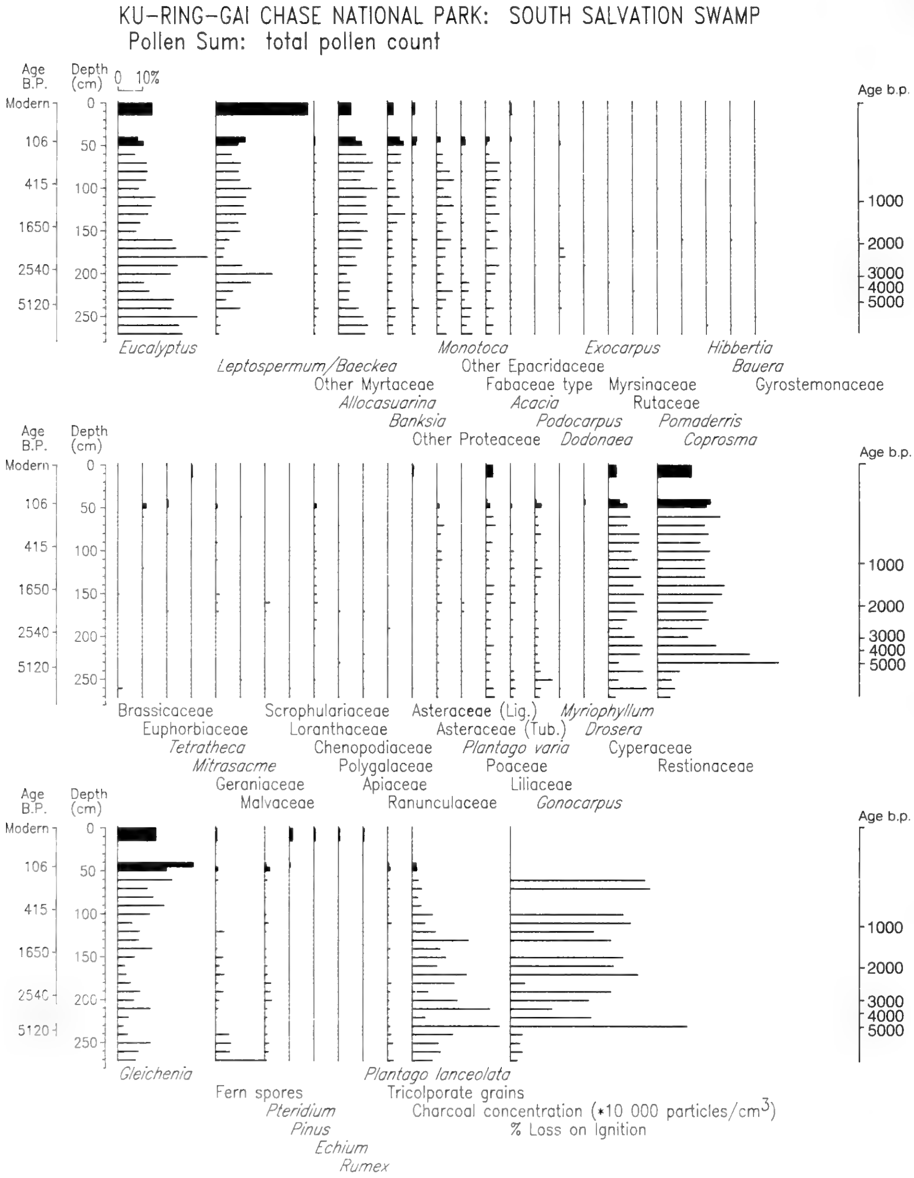

Fig. 3. Percentage pollen diagram from South Salvation Creek Swamp. In this diagram the modern sample incorporates the uppermost 15cm of sediment. Samples at 40 and 45cm represent 5cm sample thicknesses, ie. 40-45cm and 45-50cm respectively, while all other samples represent 1cm sample thicknesses at 10cm intervals.

present throughout the record. The sandstone flora has retained its sclerophyll nature, reflecting stability and therefore resilience to nutrient-poor sandy soils, high insolation

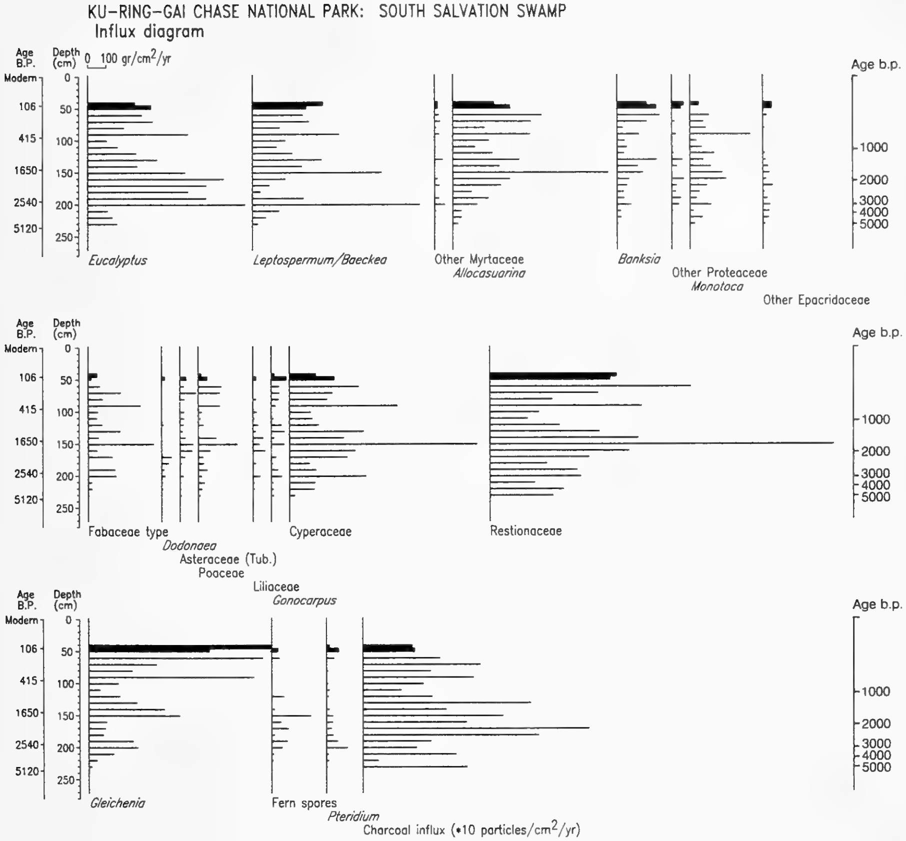

Fig. 4. Influx diagram for major pollen types from South Salvation Creek Swamp.

exposure, drought, and fire. Such vegetation is probably unlikely to be sensitive to minor environmental changes. Although the results show few or no changes in vegetation composition there are changes in relative abundances.

The pollen of many of the heath and understorey shrubs of woodland and forest communities is poorly dispersed, including that for *Acacia*, Epacridaceae, Fabaceae, Proteaceae and Rutaceae (Dodson, 1983). This explains the relatively low values for these taxa which are common in the vegetation at Ku-ring-gai Chase. Their underrepresentation in the pollen record does not reflect their true importance in the vegetation.

Fires appear to have been present throughout the record, reflecting a consistent association between fire and dry sclerophyll vegetation. There is a decline in charcoal within the last 200 years, coinciding with the arrival and settlement of European Man in the Sydney region. This may reflect the displacement of Aborigines and their burning practices. At the same time European presence is marked in the surface samples by *Echium*, *Pinus*, *Plantago lanceolata* and *Rumex* pollen.

Low loss-on-ignition values corresponding to thin sandy lenses appear with or above (indicating possible time lags) relatively high charcoal levels at around 4200 b.p.

and 2300 b.p. These are likely to indicate disturbance and erosion from the surrounding slopes.

Trends in pollen of swamp taxa show that the early swamp surface was dominated by Restionaceae, and possibly a fern other than *Gleichenia* during the more minerogenic deposition. Woody shrubs: *Banksia robur*, *Leptospermum juniperinum* and *Aotus ericoides*, prefer deeper sediments which could explain their general increases toward the present as a local successional effect. Increasing deposition would have created drier conditions on the swamp favouring their establishment and that of *Gleichenia*. Above this general trend smaller changes probably reflect local variations in water-table depth or the changing patterns of distribution of taxa by population fluctuations, interspecific competition, or fire.

Any relationship between charcoal influx and pollen abundance from swamp taxa could reflect fire adaptations of these taxa. Although normally much regeneration would be from rhizomes and suckering, the clearance of the thick *Gleichenia* and *Empodisma* cover would allow initial recruitment by seed dispersal, particularly of woody shrubs. Nutrient influx to the swamp after fires may also have some impact on the swamp vegetation. Fire may therefore be an important factor in swamp vegetation dynamics. A peak in *Leptospermum* pollen occurs with a decline in Cyperaceae, Restionaceae and *Gleichenia* around 2900 b.p. which could represent a dry period allowing *L. juniperinum* to expand on the swamp.

The initial major decline in *Eucalyptus* around 1800-1900 b.p. corresponds with a trend of increasing *Gleichenia* and swamp shrubs which may together represent climatic conditions becoming slightly drier and the eucalypt canopy opening towards a more woodland type. Alternatively the mire surface could have expanded laterally, thereby pushing back the eucalypt woodland and reducing the local eucalypt pollen input reaching the core site. *Eucalyptus* values may have been high in the past due to trees directly overhanging the site.

Chalson (1983) studied the vegetation record of Jibbon Swamp in Royal National Park south of Sydney. The site is located on a sandsheet overlying Hawkesbury Sandstone with the swamp set in the swale of a U-shaped dune about 1km from the shoreline and 10m above sea level. Chalson (pers. comm.) found *Eucalyptus* to be more common prior to about 5000 b.p. with *E. sieberi* pollen (possibly the mallee form of *E. sieberi* which occurs in the area today) highest around 4000 b.p. and declining to the present. At Kurnell Peninsula *Eucalyptus* declined after 2000 b.p. and was replaced by dune shrubs such as *Leptospermum* and *Monotoca* (Martin, 1986, and 1988 pers. comm.). These studies may suggest a regional decline in *Eucalyptus* in the late Holocene, a question worthy of further research.

The results show a very high local pollen input from plants growing on or near the swamp. For densely vegetated sites like South Salvation Creek Swamp it is difficult to separate terrestrial from swamp pollen where several genera have species representative in both habitats. For example, the source of *Leptospermum* pollen could be from the many woodland and heath species surrounding the swamp, however most of the pollen in the record is likely to be derived from *Leptospermum juniperinum* growing on the swamp. Such results emphasize the problems encountered when interpreting a pollen record derived from a complex mosaic of vegetation communities surrounding a swamp.

The lack of any consistent relationship between charcoal abundance and the behaviour of individual taxa reflects the complex relationships between vegetation and fire and the input of pollen and charcoal in the sediment. It may well be that the catchment area for charcoal differs from that of the pollen.

Plant taxa and communities are likely to have evolved and adapted to particular fire regimes rather than fire *per se* (Gill, 1975). Studying the effects of fire on vegetation requires separating the components of the fire regime (intensity, frequency, type, time of occurrence etc.) and examining these in relation to the adaptations and life cycles of the plants (Kodela, 1984). Palynological techniques cannot readily differentiate these. Nevertheless broad relationships can be established and in this case there appears to be at least an association between high *Eucalyptus* and charcoal influx; perhaps reflecting an interdependence between the eucalypt species at the site and fire.

Although sclerophyll and swamp taxa appear to have dominated the record, fluctuations in their abundances and/or distributions have occurred. These are likely to be results of a combination of factors, including water-table fluctuations, seasonal drought, fire activity, interspecific competition, the natural changing patterns in species distribution and the impact of Aboriginal and European people. Changes in swamp and terrestrial pollen taxa around 2000 b.p. may indicate a drier climate to the present.

ACKNOWLEDGEMENTS

We are grateful to Chris Myers (UNSW) for technical help, Colin Pain (UNSW) and Bob Conroy (NPWS) for advice and field assistance, Kevin Maynard and John Owen (UNSW) for cartography and Lynne Illidge for typing the manuscript. Many friends from the 1984 honours class in Physical Geography group kindly provided labour in the field. The N.S.W. National Parks and Wildlife Service (NPWS) generously provided funds for radiocarbon dating.

References

BUCHANAN, R., 1975. — The Relationship of Swamp, Shrub and Podzol Distribution to the Geology and Physiography on the West Head Peninsula. North Ryde (N.S.W.): Macquarie Univ., B.Sc. honours thesis, unpubl.

——, 1980. — The Lambert Peninsula, Ku-ring-gai Chase National Park. Physiography and the distribution of podzols, shrublands and swamps, with details of the swamp vegetation and sediments. *Proc. Linn. Soc. N.S.W.* 104: 73-94.

BUREAU OF METEOROLOGY, 1979. — Climatic Survey Sydney, Region 5, New South Wales. Canberra: Department of Science and the Environment.

CHALSON, J., 1983. — Palynology and Paleoecology of Jibbon Swamp, Royal National Park, N.S.W. Kensington (N.S.W.): Univ. of N.S.W., B.Sc. honours thesis, unpubl.

CLARK, R. L., 1982. — Point count estimation of charcoal in pollen preparations and thin sections of sediments. *Pollen et Spores* 24: 523-535.

DODSON, J. R., 1983. — Modern pollen rain in southeastern New South Wales, Australia. *Rev. Palaeobot. Palynol.* 38: 249-268.

——, GREENWOOD, P. W., and JONES, R. L., 1986. — Holocene forest and wetland dynamics at Barrington Tops, New South Wales. *Journal of Biogeography* 13: 561-585.

ERDTMAN, G., 1969. — *Handbook of Palynology.* Copenhagen: Munksgaard.

FAEGRI, K., and IVERSEN, J., 1975. — *Textbook of Pollen Analysis.* Copenhagen: Munksgaard.

FITZPATRICK, E. A., and ARMSTRONG, J., 1972. — The bioclimatic setting. *Proc. Ecol. Soc. Aust.* 7: 7-26.

GILL, A. M., 1975. — Fire and the Australian flora: a review. *Aust. For.*, 38: 4-25.

JOWSEY, P. C., 1966. — An improved peat sampler. *New Phytol.* 65: 245-249.

KODELA, P. G., 1984. — The Vegetation and Fire History of Ku-ring-gai Chase National Park. Kensington (N.S.W.): Univ. of N.S.W., B.Sc. honours thesis, unpubl.

LAMY, D. L., and JUNOR, R. S., 1965a. — An erosion survey in the Ku-ring-gai Chase and adjoining catchments. II. *J. Soil Cons. N.S.W.* 21: 159-174.

——, and ——, 1965b. — An erosion survey in the Ku-ring-gai Chase and adjoining catchments. I. Survey of the Cowan Water and Cockle Creek catchments. *J. Soil Cons. N.S.W.* 21: 94-110.

MACPHAIL, M. K., 1984. — Small-scale dynamics in an early Holocene wet sclerophyll forest in Tasmania. *New Phytologist* 96: 131-147.

MARTIN, A. R. H., 1986. — Palaeoecology, palaeolimnology, palynology and coastal environment-areas of neglect in coastal studies? *In*: E. FRANKEL, J. B. KEENE, and A. E. WALTHO, (eds), *Recent sediments in eastern Australia: marine through terrestrial.* Sydney: Geol. Soc. Aust., NSW Division, Publ. No. 2.

MOORE, P. D., and WEBB, J. A., 1978. — *An Illustrated Guide to Pollen Analysis.* London: Hodder and Stoughton.

NATIONAL PARKS AND WILDLIFE SERVICE, 1982. — *Teachers Handbook to Ku-ring-gai Chase National Park.* Sydney: National Parks and Wildlife Service of N.S.W.

OUTHRED, R., LAINSON, R., LAMB, R., and OUTHRED, D., 1985. — A floristic survey of Ku-ring-gai Chase National Park. *Cunninghamia* 1: 313-338.

PIDGEON, I. M., 1937. — The ecology of the central coastal area of New South Wales. I. The environment and general features of the vegetation. *Proc. Linn. Soc. N.S.W.* 62: 315-340.

THOMAS, J., and BENSON, D. H., 1985. — *Vegetation Survey of Ku-ring-gai Chase National Park.* Sydney: National Herbarium of New South Wales.

APPENDIX

THE LIKELY ORIGINS OF THE MAIN TAXA IN THE POLLEN DIAGRAMS

Taxa identified in the pollen and spore record	The main or most likely genera and species represented by the preserved pollen and spores, and their ecology
Eucalyptus (includes *Angophora* spp.)	*Eucalyptus haemastoma*, *E. gummifera*, *E. oblonga*, *E. punctata*, *E. umbra*, *Angophora costata* etc. Forest and woodland trees.
Leptospermum/Baeckea	Would include *Leptospermum juniperinum* which grows on the swamp, *L. squarrosum* which occurs in moist heath communities and *Baeckea* spp., etc which occur in heath communities or as understorey shrubs in woodland and forest communities.
Myrtaceae (other)	Shrubs including *Kunzea*, *Callistemon* and *Melaleuca*.
Allocasuarina	*A. distyla* (tall shrub to small tree in moist or dry heath communities), *A. torulosa*, and *A. littoralis* (trees in sheltered forest and woodland communities).
Banksia	*Banksia robur* (shrub growing on the swamp), *B. serrata*, *B. marginata* and *B. spinulosa* (common shrubs in woodland and heath communities), *B. ericifolia* (moist heath shrub).
Proteaceae (other)	*Hakea teretifolia* (moist heath shrub) *Isopogon anethifolius*, *Petrophile pulchella*, *Conospermum* spp., *Grevillea* spp. etc. Shrubs in the forest, woodland and heath formations.
Monotoca	*Monotoca elliptica*, *M. scoparia*. Shrubs in woodlands and heath.
Epacridaceae (other)	Some species occur on the swamp margin e.g. *Sprengelia incarnata*. *Leucopogon* (low heath or woodland shrub) encountered several times in the pollen record.
Fabaceae	*Aotus ericoides* (woody shrub growing on the swamp) and many heath and woodland species such as *Dillwynia* spp., *Pultenaea* spp., *Bossiaea* spp., *Phyllota phylicoides*.
Euphorbiaceae	Mainly *Amperea xiphoclada* (low shrub)
Liliaceae	*Xanthorrhoea* spp., *Thysanotus* spp., *Dianella* spp. Herbs in heath, woodland and forest communities.
Gonocarpus	*G. tetragynus*, *G. teucrioides*, *G. micranthus*. Herbs in heaths and forests.
Cyperaceae	*Gahnia sieberiana*, *Lepidosperma* spp., *Gymnoschoenus sphaerocephalus*, *Caustis* spp. Swamp and moist heath sedges.
Restionaceae	*Empodisma minus*, *Restio* spp. Swamp herbs. (Also on moist rock shelves and in moist heaths).
Gleichenia	*Gleichenia dicarpa*. Fern growing on swamp and in other moist areas.
Pteridium	*Pteridium esculentum*. Often increases with disturbance.
Fern spores	These include *Cyathea*, *Lycopodium*, *Blechnum*, Polypodiaceae, *Adiantum* and *Selaginella*. Understorey species in moist forests, near creeks, moist rock crevices, etc.
Pinus	*Pinus radiata*. Introduced trees.

A new Species of *Melita* (Crustacea: Amphipoda: Melitidae) from northern New South Wales with a Note on the Genus *Abludomelita* Karaman, 1981

W. ZEIDLER
(Communicated by F. W. E. ROWE)

ZEIDLER, W. A new species of *Melita* (Crustacea: Amphipoda: Melitidae) from northern New South Wales with a note on the genus *Abludomelita* Karaman, 1981. *Proc. Linn. Soc. N.S.W.* 110 (4), (1988) 1989: 327-338.

A new species of *Melita* from a small, artificial, freshwater coastal lake at Angourie, northern N.S.W. is described. It was found with other fauna characteristic of the larger coastal rivers of eastern Australia. It is most similar to the New Zealand species *M. awa* Barnard, 1972, but does not share the same pleonal tooth formula. *M. festiva* (Chilton 1885), the only Australian species with the same pleonal tooth formula, differs primarily in the form of the gnathopods and the small posteroventral tooth of the third pleonal epimeron. The new species does not readily fit into either *Melita* or *Abludomelita* as defined by Karaman (1981) and the division of *Melita* into the above two genera is considered unjustified without a more detailed revision.

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INTRODUCTION

There has been no comprehensive study of the genus *Melita* in Australia and of the 61 species listed by Barnard and Barnard (1983) only four have been recorded from Australia. Sheard (1937) only listed *M. festiva* and *M. fresneli* (now in *Dulichiella*). Barnard (1972) described two new species, *M. matilda* and *M. oba* and a new subspecies of *M. zeylanica* (*keuerti*) all from south Western Australia but did not list any other species of *Melita*. *M. zeylanica*, a cosmopolitan species, has been recorded from Australia more recently by Collett *et al.* (1981). Kangas and Geddes (1984), Poore (1982) and Potter *et al.* (1981).

The species described here was found in a small, coastal, freshwater lake (actually a water-filled, disused quarry), known as 'The Blue Pools', at Angourie, 5km south of Yamba, northern New South Wales. It was found near the shallow edges together with a small hydrobiid snail (*Posticobia brazieri*) and the hymenosomid crab (*Amarinus lacustris*) both of which are characteristic of the fauna of larger coastal rivers of eastern Australia.

MATERIALS AND METHODS

Specimens were collected from the shallow edges of only one of the two small freshwater lakes at Angourie. The species was not particularly abundant and only 10 males and 5 females were collected. I was unable to obtain specimens from coastal rivers nearby and no additional material was available from the Australian Museum, Sydney.

The holotype male and allotype female are deposited in the Australian Museum, Sydney (AM), and the remainder, all designated paratypes, are deposited in the South Australian Museum, Adelaide (SAM).

Specimen length was measured along a lateral parabolic line drawn from the anterior extremity of the head through the middle of the body to the posterior limit of pleonite 6.

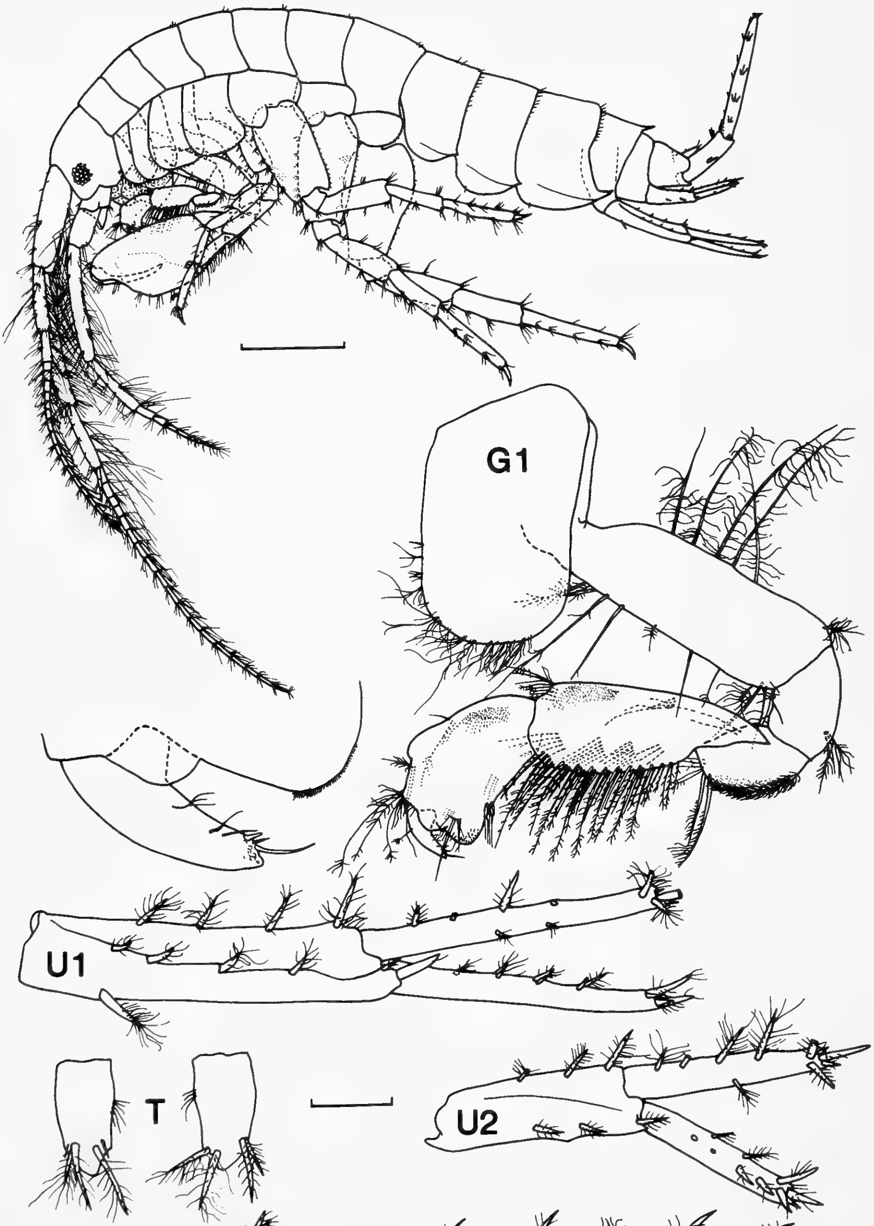

Fig. 1. Melita plumulosa sp. nov. Holotype male; scale bars = 1mm and 0.2mm respectively. Abbreviations used in figures and text: A1, antenna 1: A2, antenna 2; Mxp, maxilliped; Mx1, maxilla 1; Mx2, maxilla 2; Md, mandible; UL, upper lip; LL, lower lip; G1, gnathopod 1; G2, gnathopod 2; P3-P7, pereopod 3 to pereopod 7; U1-U3, uropod 1 to uropod 3; T, telson; P14, P15, fourth and fifth pleonite; R, right; L, left.

Unless indicated otherwise dissected appendages were taken from the left hand side of the animal. All specimens and dissected appendages are preserved in 2% formaldehyde/propylene glycol solution.

Material examined

Holotype ♂ (AM, P37289), allotype ♀ (AM, P37290) and 11 paratypes (9 ♂, 4 ♀) (SAM, C4076), all from the shallow edges of the northern-most pond (freshwater) of 'The Blue Pools' at Angourie, 5 km south of Yamba, N.S.W., collected by W. Zeidler, 4.1X.1984.

Also examined were all specimens of *Melita* in the collections of AM and SAM.

DESCRIPTION

Melita plumulosa sp. nov.

(Figs 1-5)

DESCRIPTION OF HOLOTYPE: Male 6.7mm (AM, P37289).

Head (Fig. 1): Rostrum absent, length slightly less than first two pereonites combined; lateral cephalic lobes evenly rounded; post-antennal sinus short; eyes black, ovato-circulate.

Antenna 1 (Fig. 2): Almost as long as body; all articles with long irregularly plumulose setae particularly on posterior margin; article 1 about 80% length article 2, expanded near base with three ventral spines; article 3 short, about half length article 2; accessory flagellum 3-articulate plus tiny fourth article (2 + 1, L); flagellum with 18 + (R, broken), 17 (L) articles.

Antenna 2 (Fig. 3): Little more than half length antenna 1 with similar but generally longer setae; gland cone enlarged reaching mid-way peduncular article 3; penduncular article 4 longest almost twice length article 5; flagellum with 9 articles (L & R) together about ¾ length peduncular article 4.

Upper Lip (Fig. 4): Broader than long, apically rounded, bearing numerous short setae distally.

Lower Lip (Fig. 4): Inner lobes barely developed; outer lobes with medial tooth-like projection and fringe of short setae.

Mandibles (Fig. 4): Palp 3-articulate, article 2 about twice length article 1 with one long plumulose seta medially, article 3 slightly shorter than 2 with three short and one very long plumulose seta terminally; incisor with five teeth; lacina mobilis with four teeth; spine row with four spines, the one nearest lacina mobilis spatulate; molar triturative with one long plumulose seta.

Maxilla 1 (Fig. 4): Inner lobe with six apical plumulose setae; outer lobe with six apical trifurcate spines; palp 2-articulate with dilated, distal article armed with six terminal teeth and eight sub-terminal setae.

Maxilla 2 (Fig. 4): Inner lobe shorter and narrower than outer with about twenty setae apically and marginally; outer lobe with about twelve strong apical setae.

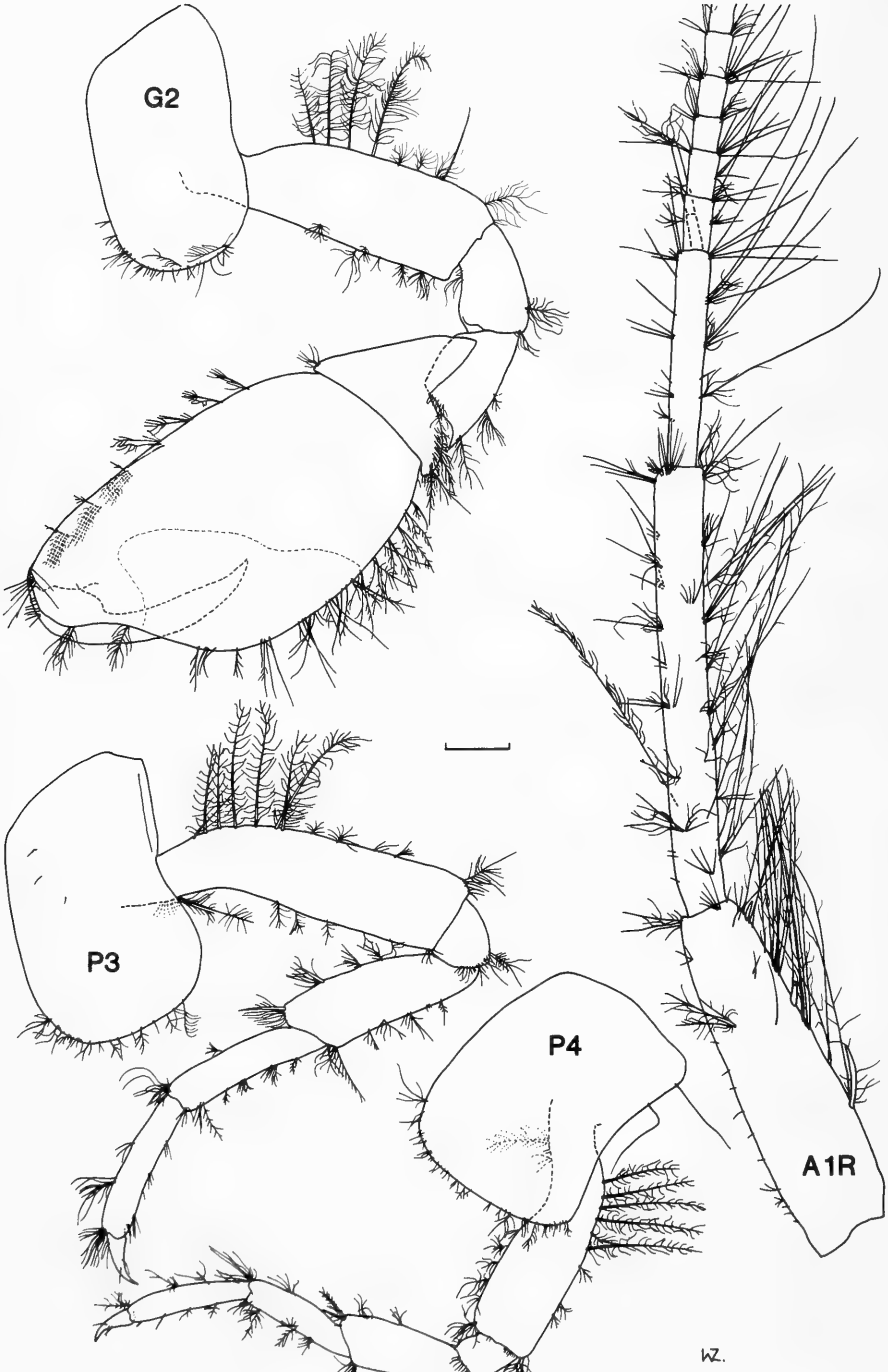

Fig. 2. Melita plumulosa sp. nov. Holotype male; scale bar = 0.2mm. See legend to Fig. 1 for key to abbreviations.

Maxilliped (Fig. 4): Inner lobe reaching ¼ along article 2 of palp bearing several setae apically and along inner margin; outer lobe reaching 3/5 along article 2 of palp, semicircular about half as wide again as inner lobe with seven apical feathered setae and two rows of shorter setae along inner margin interspersed with bristles; palp article 2 with plumulose setae along inner margin, article 3 about ⅔ length article 2 dilated distally with patch of close-set bristles on inner distal corner and four long setae on outer distal corner, article 4 unguiform, subequal to article 3 with terminal nail and fringe of short setae on inner margin.

Gnathopod 1 (Fig. 1): Coxal gill absent; coxa with plumulose setae on lower and distal half of anterior margin; article 6 is 60% length article 5 with anterior hump, palm transverse with medial hump extending to outer margin of dactylus; dactylus curved, blunt with three strong setae on postero-distal corner, shorter than width of palm.

Gnathopod 2 (Fig. 2): Less setose and much larger than gnathopod 1; coxal gill sac-like, slightly longer than wide, as long as article 2 with very convex posterior margin and almost straight anterior margin; coxa slightly larger but like that of gnathopod 1; article 4 with sharp posterodistal extension; article 6 unlobed, large, about ¾ length articles 2-5 combined, palm oblique with few scattered plumulose setae otherwise smooth and undefined by teeth or processes; dactylus smooth length equal to width article 6, overriding palm on inside face, fitting into weak undefined hollow.

Pereopod 3 (Fig. 2): Slightly shorter than gnathopod 2; coxal gill like that of gnathopod 2 but slightly longer and narrower; coxa slightly larger than that of gnathopod 2 with slightly concave posterior margin; articles 5 and 6 subequal in length slightly shorter than article 4; all articles sparsely setose.

Pereopod 4 (Fig. 2): About ⅔ length pereopod 3 otherwise similar except for following; coxa more rectangular, wider and shorter; article 6 slightly longer than article 4 or 5 which are subequal in length.

Pereopod 5 (Fig. 3): About twice length pereopod 4; coxal gill oval-shaped, smaller than that of pereopod 4, about ⅔ length article 2; coxa wider than article 2 with large anterior lobe equivalent to about 40% of total coxal length and small posterior lobe; article 2 rectangular about ⅔ as wide distally as proximally with conical posterodistal projection; article 6 about 1¼ times length article 5 and slightly longer than article 4; all articles except dactylus with sparsely spaced plumulose spines.

Pereopod 6 (Fig. 3): Similar to pereopod 5 but about 10% longer; coxal gill smaller only slightly longer than ½ article 2; coxa with small anterior lobe and no posterior lobe but with small posterodistal projection; article 6 relatively longer than for pereopod 5.

Pereopod 7 (Fig. 3): 10% longer than pereopod 6 and longest pereopod; coxal gill absent; coxa semilunate about twice as wide as long; article 2 proximally expanded and distally narrowed; articles 4 and 5 subequal in length about ¾ length article 6; otherwise similar to pereopod 6.

Pereon: Without dorsal or lateral projections.

Pleon (Figs 1 and 4): Pleonal epimera with lateral ridge, 1-2 with small (3 with large) posteroventral tooth, dorsally smooth, all with minor serrations on ventral margin and

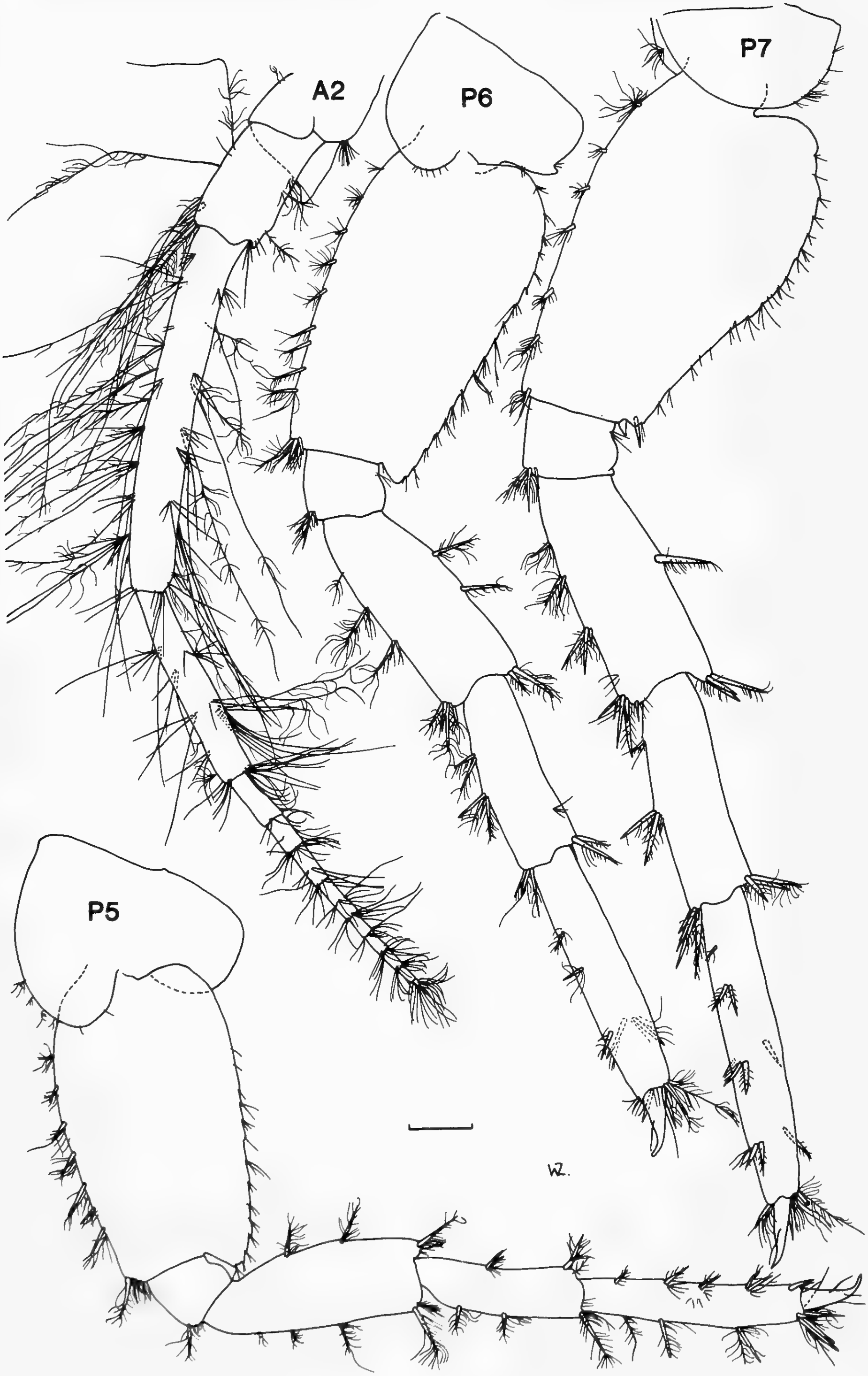

Fig. 3. Melita plumulosa sp. nov. Holotype male; scale bar = 0.2mm. See legend to Fig. 1 for key to abbreviations.

2-3 with small spine near anteroventral corner; pleonite 4 bearing large dorsal tooth projecting posteriorly to limit of pleonite 5; pleonite 5 with one dorsolateral tooth on each side accompanied by one dorsally placed, upwardly curved spine; pleonite 6 gently rounded posteriorly with dorsal depression near base of telson and acute lower posterior corner.

Uropod 1 (Fig. 1): Reaching to ¼ length of outer ramus of uropod 3; rami subequal slightly shorter than peduncle each tipped with three large and two small spines; inner and outer margins of peduncle and rami spinulated; peduncle with large spine at insertion of outer ramus and proximally on lower margin almost ¼ along length of peduncle.

Uropod 2 (Fig. 1): Shorter than uropod 1; outer ramus slightly shorter than inner, both armed similarly to uropod 1; peduncle as long as inner ramus, inner and outer margins with three large spines.

Uropod 3 (Fig. 1): Greatly elongate; outer ramus about twice length peduncle, bearing bunches of spines along both margins, with spine-like distal article surrounded by five smaller spines; inner ramus short, scale-like about ⅓ length peduncle with one large subterminal spine; peduncle with one small and one large spine mid-ventrally, four spines on posteroventral corner, two spines on outer posterodorsal corner and three spines near inner posterodistal corner.

Telson (Fig. 1): About ½ or less length peduncle uropod 3, cleft to base, outer margins rounded, inner margins slightly excavate for terminal ¼; each lobe with two large subapical spines near inner and outer margin on dorsal surface.

DESCRIPTION OF ALLOTYPE: Ovigerous female 4.7mm (AM, P37290) with eleven eggs in brood pouch.

Differs from male as follows: Setae and spines of appendages not plumulose.

Antenna 1 (Fig. 5): Setae not as long or as numerous; accessory flagellum 2-articulate plus tiny third article; flagellum with 17 articles.

Antenna 2 (Fig. 5): Gland cone relatively larger, reaching ¾ along peduncular article 3; peduncular article 4 only marginally longer than article 5; flagellum with 7 articles together slightly longer than peduncular article 4.

Coxae: Slightly more elongate.

Gnathopod 1 (Fig. 5): Article 6 without humps; dactylus as long as palm.

Gnathopod 2 (Fig. 5): Only slightly larger than gnathopod 1; article 6 slightly longer than article 4 and 5 combined, palm oblique undefined by teeth or processes; dactylus not over-riding inner face of palm.

Pereopod 6 (Fig. 5): Coxa with relatively long anterior lobe almost as long as rest of coxa.

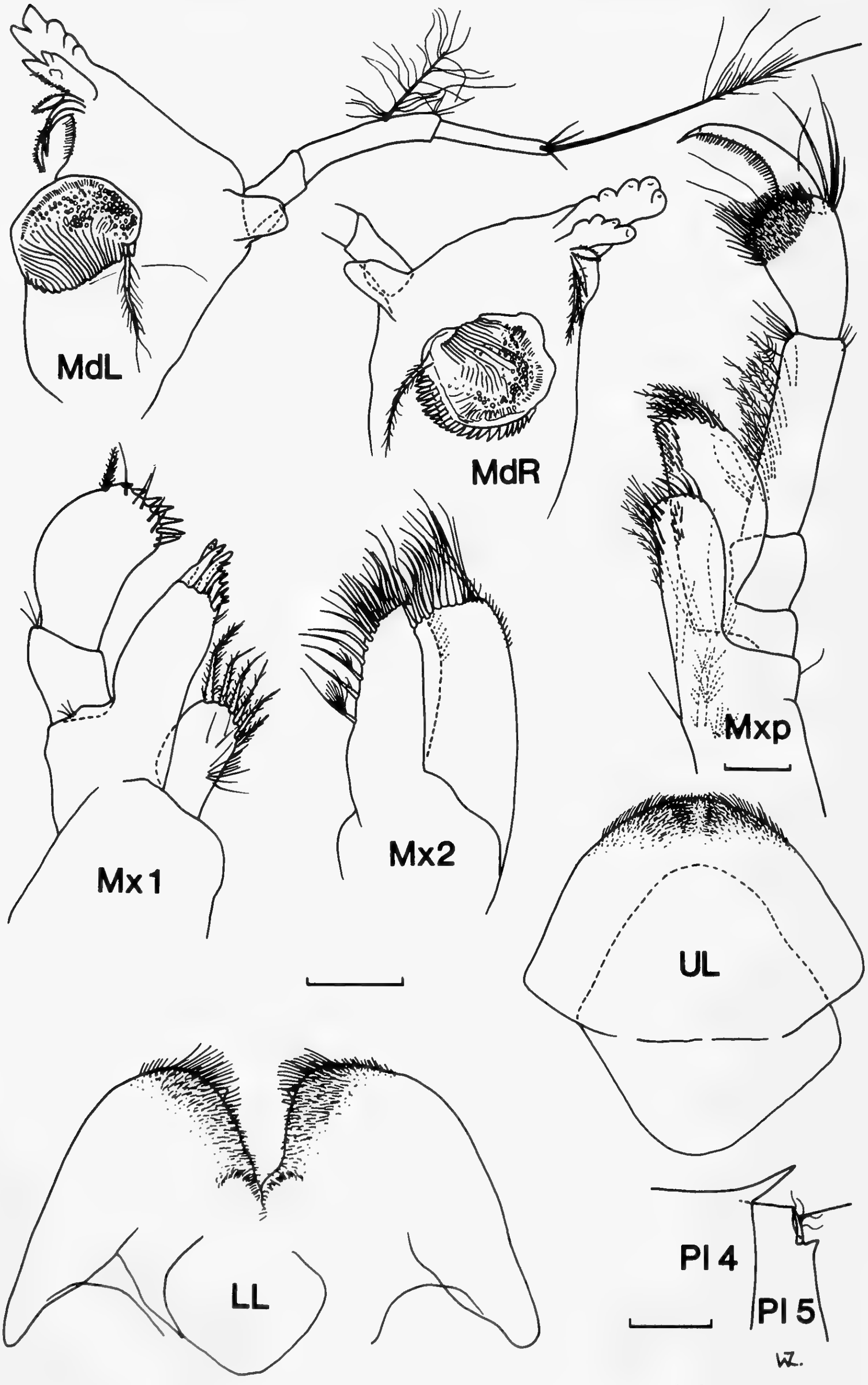

Fig. 4. Melita plumulosa sp. nov. Holotype male; scale bars = 0.1mm and 0.2mm respectively. See legend to Fig. 1 for key to abbreviations.

Oostegites (Fig. 5): On gnathopod 2 and pereopods 3-5, very slender with sparse marginal setae, all similar in shape and size.

Uropod 1: Reaching less than ¼ length outer ramus uropod 3.

Paratypes: 9 males, 4 females (SAM, C 4076) show little variation from the holotype or allotype. In some specimens pleonal epimera 2 and 3 have two anteroventral spines. The spines and setae of the males are not as plumulose as in the holotype and of the four females one is ovigerous with spines and setae like the allotype, the other three have some spines and setae plumulose as in the males.

Etymology: The name refers to the irregularly plumulose nature of the spines and setae.

DISCUSSION

M. plumulosa is only known from the type locality. 'The Blue Pools' at Angourie were formed as a result of quarrying in the 1920s, the resultant excavation having filled with freshwater from groundwater discharge and surface run-off. Thus colonization has taken place recently and one would expect to find the species in coastal rivers nearby. There are two main lakes at Angourie both less than 100m from the sea but amphipods were only found in the northern one. This lake is the smaller of the two, about 20m in diameter and about 8m deep. Although the habitat is very close to the sea and would be affected by salt spray the surface water is always fresh (C. Creighton pers. comm.) but stratification may occur with brackish water being kept near the bottom.

A distinctive feature of *M. plumulosa* is the irregularly plumulose character of the spines and setae, more developed in males, and common to all parts of the animal including the mouthparts. I have been unable to find this character in any of the species of *Melita* that I have examined nor could I find a reference to it for any other species of *Melita* or indeed for any species of gammaridean amphipod. Another unusual feature is the humps on article 6 of the first male gnathopods, a character which appears to be rare amongst melitids and apart from *M. awa* Barnard, 1972, does not occur in any other species although some such as *M. hergensis* Reid, 1939, and *M. palmata* (Montague, 1804) have the first male gnathopods with the anterodistal margin broadly rounded to overlap the base of the dactylus.

M. plumulosa is most similar to the New Zealand species *M. awa*, particularly in the form of the gnathopods. However, apart from several minor differences, *M. awa* is distinguished from *M. plumulosa* by the lack of a dorsal spine on pleonite 4; in that the posteroventral angle of epimeron 3 consists of a small tooth and that the telson is slightly longer than half of the peduncle of uropod 3.

In Australia this species must be compared with *M. festiva* (Chilton, 1885) with which it shares the same pleonal tooth formula. *M. festiva* differs from *M. plumulosa* in several characters but mainly in (1) the shape of article 6 of the male gnathopod 1 which lacks humps and is about twice as long as wide; (2) the large size of article 6 of the male gnathopod 2 which is longer than the rest of the limb and also the distinct teeth on the palm; (3) the relatively short, blunt dactylus of the male gnathopod 2 which arises from article 6 off-centre; (4) the irregularly toothed palm of the female gnathopod 2; (5) the small posteroventral tooth of epimeron 3; and (6) the telson length which is equivalent to the peduncle of uropod 3.

Other species (none Australian) which also share the same pleonal tooth formula are *M. abyssorum* Stephenson, 1944, *M. hergensis*, *M. palmata* and *M. planaterga* Kunkel,

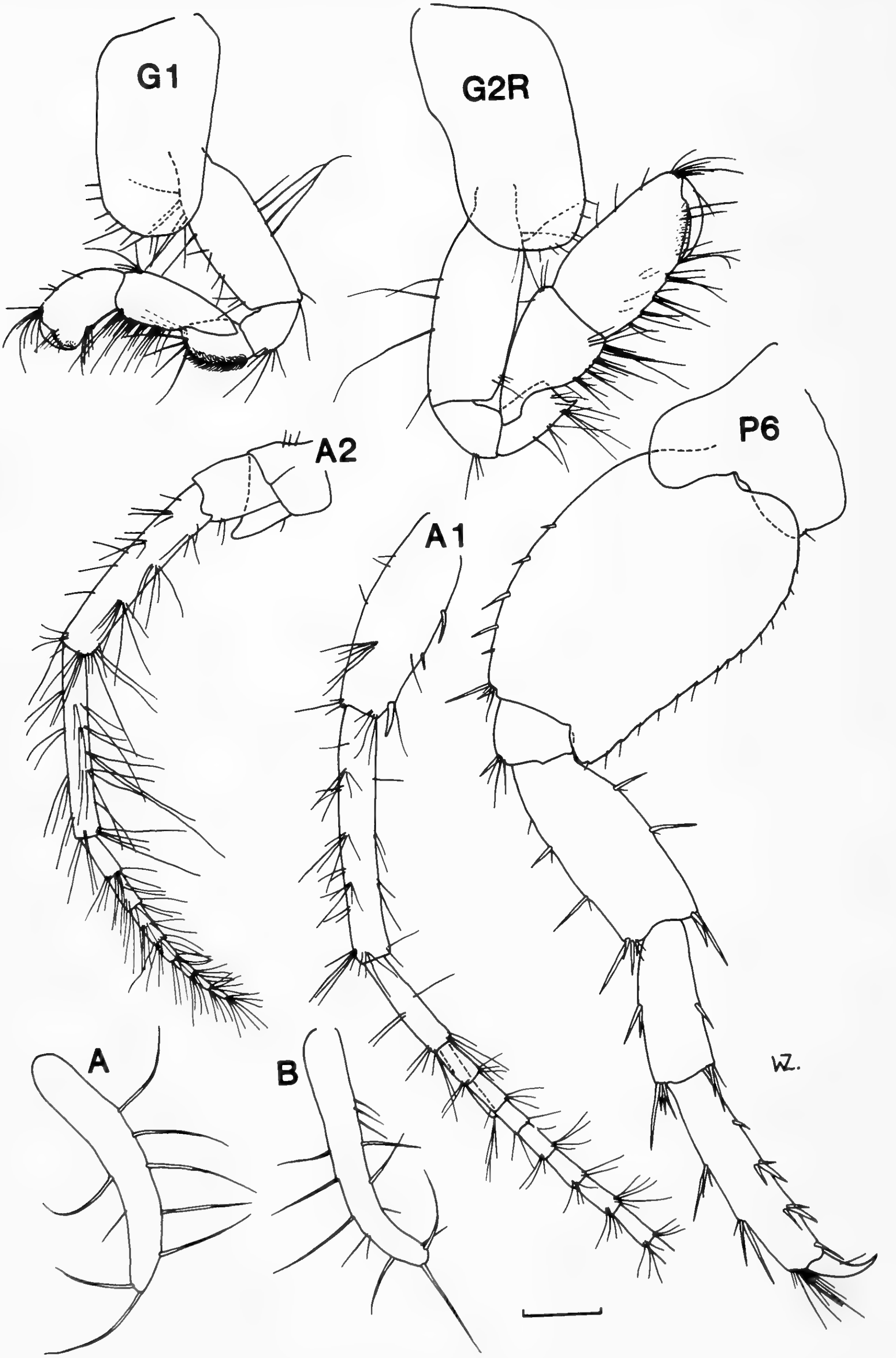

Fig. 5. Melita plumulosa sp. nov. Allotype female; A and B, oostegite from G2 and P5 respectively; scale bar = 0.2mm.
See legend to Fig. 1 for key to abbreviations.

1910. These species differ from *M. plumulosa* in the following main characters. In *M. abyssorum* the eyes are absent and the male gnathopod 2 has a large palmar tooth. In *M. hergensis* article 6 of the male gnathopod 1 has the anterodistal margin broadly rounded to overlap the base of the dactylus and the inner surface of the palm of gnathopod 2 is finely setose. In *M. palmata* the male gnathopod 1 is similar to *M. hergensis* as is the setation of gnathopod 2 but in addition article 6 is very broad distally. In *M. planaterga* the male gnathopod 1 is similar to *M. hergensis*, the male gnathopod 2 is very setose, article 2 of pereopods 5-7 is inflated and rounded and the posteroventral angle of epimeron 3 consists of a medium tooth.

It is worth noting here that Barnard (1962) lists *M. planaterga* as a species without dorsal epimeral spines however Karaman (1981) clearly illustrates epimeral spines similar to those of *M. plumulosa* as do Lazo-Wasem and Gable (1987) who redescribed *M. planaterga* from recently-discovered type material, although they regard Karaman's specimen as a different and possibly undescribed species.

Apart from the pleonal tooth formula and the absence of humps on article 6 of the male gnathopod 1, other Australian species differ from *M. plumulosa* principally in the following manner. In *M. matilda* Barnard, 1972 (1) the accessory flagellum of antenna 1 consists of 5 articles; (2) the palm of the male gnathopod 2 has a deep hollow with spines to accommodate the dactylus; (3) the female coxa 6 is unmodified; (4) the posterodistal angle of article 2 of pereopods 5-7 is not produced; (5) the setae and spines on uropod 3, and at least some on articles 4-6 of pereopods 5-7, are about twice as long; (6) mandibular palp article 3 is longer than article 2. In *M. oba* Barnard, 1972 (1) the accessory flagellum of antenna 1 consists of 4-5 articles; (2) the medial face of the male gnathopod 2 is very setose and there is no hollow for the dactylus which only partly over-rides the palm; (3) article 4 of the female gnathopod 2 is without a sharp process; (4) coxa 4 is expanded ventrally and slightly excavate; (5) article 2 of pereopods 5-7 is more regularly ovate with rounded postero-distal lobes; (6) the posteroventral angle of epimeron 3 is only slightly produced; (7) mandibular palp article 3 is longer than article 2. In *M. zeylanica* Stebbing, 1904 (1) the medial face of the palm of the male gnathopod 2 is very setose; (2) coxa 4 is deeply excavate posterodistally; (3) article 2 of pereopods 5-7 is inflated and rounded; (4) the posteroventral angle of epimeron 3 consists of a small tooth.

NOTE ON THE GENUS *ABLUDOMELITA* KARAMAN, 1981

In his study of the genus *Melita*, Karaman (1981) determined two groups of species, those 'without dorsal oblique row of setae on inner lobe of maxilla 2 and prevalently with 1- segmented outer ramus of uropod 3' and those 'with dorsal oblique row of setae on inner lobe of maxilla 2 and prevalently with 2- segmented outer ramus of uropod 3'. Karaman considered these characters to be of generic significance and consequently erected the genus *Abludomelita* to accommodate the latter group, the former being retained in the genus *Melita*.

In *M. plumulosa* the inner lobe of maxilla 2 is without a dorsal oblique row of setae and the outer ramus of uropod 3 can be considered 2-segmented. Thus following Karaman it could be placed into either of the above two groups. Based on the character of maxilla 2 alone *M. plumulosa* would fit into the *Melita* group but this would deny its close relationship to *M. awa* which is placed in the *Abludomelita* group by Karaman.

As the two characters on which *Abludomelita* is based are plesiomorphic the genus is at best paraphyletic and probably polyphyletic. The setation of maxilla 2 has not been critically examined for most species of *Melita* and the degree of variation is unknown. Also I do not consider the loss of article 2 on the outer ramus of uropod 3 to be of generic significance in *Melita* as this article can be so reduced in some species that it is hidden by, or is indistinguishable from, adjacent spines (i.e. when is an article just another spine?). Karaman admits that the 'pilosity of maxilla 2 is not described in some species' and that some of his conclusions are based solely on the form of uropod 3. Clearly *Melita* needs much more detailed study before new generic concepts are put forward.

In consideration of the above I am reluctant to accept Karaman's division of *Melita* and his new genus *Abludomelita* until a more detailed revision of the genus is undertaken. In the meantime I am referring my species to the genus *Melita*.

Of the species mentioned in this paper Karaman transferred the following to *Abludomelita*: *M. abyssorum, M. awa, M. festiva, M. matilda* and *M. oba*.

ACKNOWLEDGEMENTS

I wish to thank Mr C. Creighton of Landwater Management, Angourie, and Dr B. V. Timms, Avondale College, Cooranbong, N.S.W. for information regarding the type locality. Dr W. F. Ponder, The Australian Museum, Sydney, identified the hydrobiid snail. Dr J. K. Lowry, The Australian Museum, Sydney, kindly reviewed the manuscript and provided comparative material for this study.

References

BARNARD, J. L., 1962. — Benthic marine Amphipoda of southern California: Families Tironidae to Gammaridae. *Pacific Nat.* 3: 73-115.

——, 1972. — Gammaridean Amphipoda of Australia, Part I. *Smithson. Contrib. Zool.* 103: 1-333.

——, and BARNARD, C. M., 1983. — *Freshwater Amphipoda of the World.* 2 Vols. 830 pp. Mt Vernon, Virginia: Hayfield Associates.

COLLETT, L. C., COLLINS, A. J., GIBBS, P. J., and WEST, R. J., 1981. — Shallow dredging as a strategy for the control of sublittoral macrophytes: a case study in Tuggerah Lakes, New South Wales. *Aust. J. Mar. Freshw. Res.* 32: 563-571.

KANGAS, M. I., and GEDDES, M. C., 1984. — The effects of salinity on the distribution of amphipods in The Coorong, South Australia, in relation to their salinity tolerance. *Trans Roy. Soc. S. Aust.* 108(3): 139-145.

KARAMAN, G. S., 1981. — Redescription of *Melita planaterga* Kunkel 1910 from Bermuda islands with revision of genera *Melita* Leach and *Abludomelita* n. gen. *Poljoprivreda i Sumarstvo,* Titograd 27(1): 29-50.

LAZO-WASEM, E. A., and GABLE, M. F., 1987 — A review of recently discovered type specimens of Bermuda Amphipoda (Crustacea: Peracarida) described by B. W. Kunkel (1882-1969). *Proc. Biol. Soc. Wash.* 100(2): 321-336.

POORE, G. C. B., 1982. — Benthic communities of the Gippsland Lakes, Victoria. *Aust. J. Mar. Freshw. Res. 33*: 901-915.

POTTER, I. C., LENANTON, R. C. J., LONERGAN, N., CHRYSTAL, P., CAPUTI, N., and GRANT, C., 1981. — The fish and crab fauna of the Peel-Harvey estuarine system in relation to the presence of *Cladophora.* Bull. No. 88. Dept. Cons. Env. W.A.

SHEARD, K., 1937. — A catalogue of Australian Gammaridea. *Trans Roy. Soc. S. Aust. 61*: 17-29.

Baseline Survey of the Benthic Macrofauna of Twofold Bay, N.S.W., with a Discussion of the Marine Species introduced into the Bay

PAT HUTCHINGS, JOS VAN DER VELDE, and STEVE KEABLE

HUTCHINGS, P. A., VAN DER VELDE, J. T., and KEABLE, S. J. Baseline survey of the benthic macrofauna of Twofold Bay, N.S.W., with a discussion of the marine species introduced into the Bay. *Proc. Linn. Soc. N.S.W.* 110 (4), (1988) 1989: 339-367.

A baseline survey of the benthic macrofauna of Twofold Bay, southern N.S.W., was carried out during 1984-85. Sampling was concentrated in intertidal and shallow subtidal habitats. Samples were collected seasonally and, although sampling was largely qualitative, some attempts were made to assess the abundance of species and this is indicated in the species list given.

The survey originated in response to a study on ballast water which is regularly discharged into Twofold Bay (Williams *et al.*, 1988). The ballast water contained living organisms and Williams *et al.* (1988) suggested that these animals could survive discharge into the Bay.

The purpose of this survey was to conduct a baseline study of the macrofauna of Twofold Bay and to determine if any non-indigenous species had been introduced into the bay. Seven introduced species were found and the possible methods by which these became established in the bay are discussed.

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INTRODUCTION

Background to Study

During the 1970s considerable concern was expressed both overseas and in Australia on the likelihood of marine introductions via ballast water discharged into ports. Subsequent colonization and the potential for the development of them to become 'pest' species was also of concern (Friese, 1973; Medcof, 1975; Medcof and Wolf, 1975). Carlton (1985, 1987) has recently reviewed species introduced via ballast water on a world wide basis.

In response to this concern primarily within the fishing industry, the then New South Wales Department of Fisheries, now the Department of Agriculture and Fisheries, undertook a survey of the ballast water of Japanese ships discharging ballast water into selected Australian ports. Their survey revealed a variety of living organisms in the ballast water belonging to a number of groups, including 8 non-indigenous species (6 copepods, 1 mysid and 1 amphipod) and an additional 14 species of copepods and 4 non copepod taxa with an Indo-Pacific distribution. Twenty one copepods and 22 other species, from the ballast water sampled, could not be identified to species. Sediment in the bottom of the ballast water tanks contained 8 non-indigenous species, 8 cosmopolitan and 27 other taxa not identified (Williams *et al.*, 1988). They determined by experiments that such organisms could survive discharge through the pumps into the water and thus could possibly settle and establish populations in an Australian port.

Twofold Bay on the south coast of New South Wales (37°05′S, 149°54′E) is one of the ports identified by Williams *et al.* (1988) as receiving ballast water containing living organisms on a regular basis from northern Japan during loading of woodchips at the wharf on the southern shores of the bay. Medcof (1975), in an earlier survey had also found living ostracods, crustacean larvae, adult and larval polychaetes and chaetognaths in ballast water of a woodchip carrier at Eden, Twofold Bay.

Twofold Bay has been a port since the late 1800s, for a variety of goods including whale products, gold, agricultural produce and most recently for woodchip (Matthews, 1947). Thus considerable scope has existed for introductions via fouling organisms on the bottoms of ships and more recently via ballast water (Medcof 1975; Williams *et al.*, 1988). The marine fauna of the bay has not however been documented.

During 1984 and 1985, The Australian Museum undertook a baseline study of Twofold Bay as a follow-up to the survey of Williams *et al.*, 1988. The aims of the survey were (1) to document the macrobenthic fauna of the area, and (2) identify any marine introductions. Any species recognized as non-indigenous to the area, could then be the subject of a subsequent study, to assess what impact, if any, this species is having on the natural fauna and recommend control measures. This baseline study will also facilitate the documentation of any subsequent introductions.

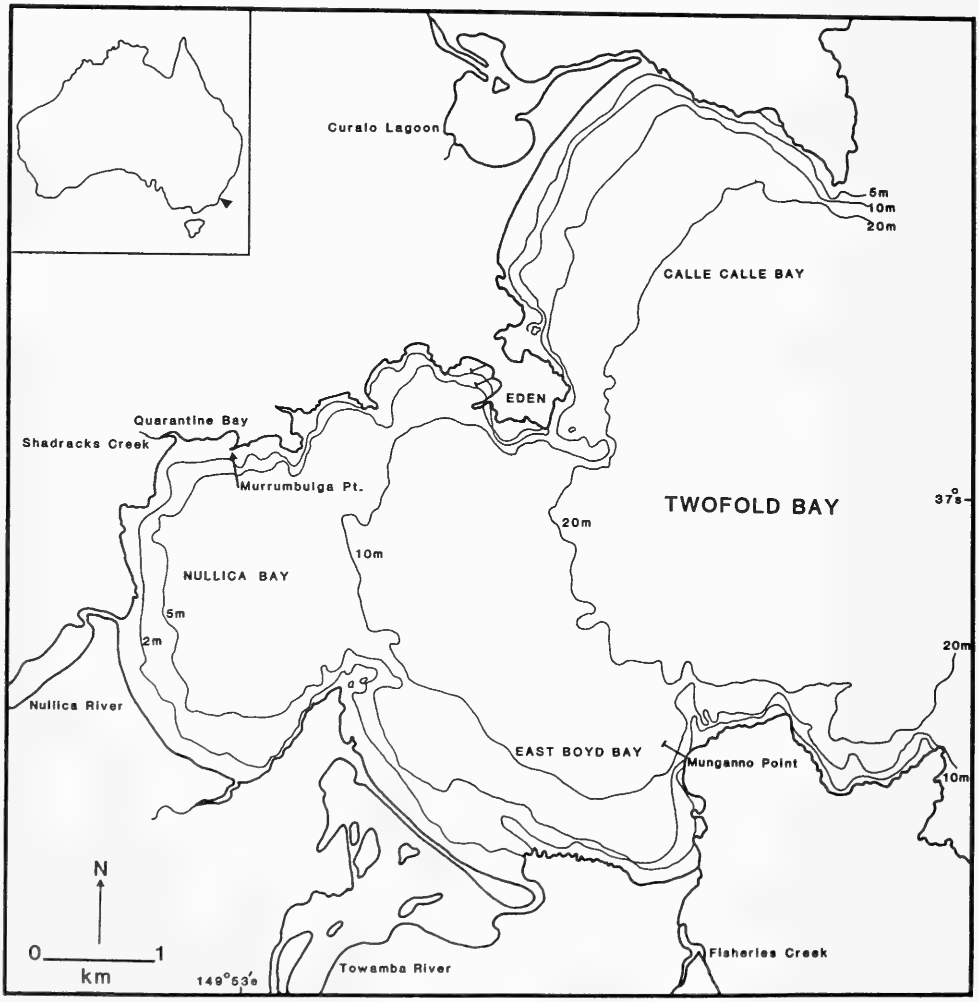

Fig. 1. Map showing location of sampling sites within Twofold Bay.

Study Area

Twofold Bay is a large open bay, consisting of 3 smaller bays, Calle Calle, Nullica and East Boyd Bay (Fig. 1). The headlands and corresponding rock platforms are of

Devonian sedimentary strata. The beaches between these bays are mini-barrier dune systems which form Curalo Lagoon and are also evident at the mouth of Fisheries Creek, Towamba and Nullica Rivers.

Rationale for sampling strategy

Ballast water is usually taken on board after unloading the cargo. Ports are usually sited in estuarine or shallow protected bays so that the fauna taken on board with the ballast water is primarily permanent estuarine plankton and planktonic larval stages of estuarine or shallow water species. The adults of such species tend to live as encrusting organisms or benthic organisms in soft sediment or seagrass communites, therefore sampling was concentrated in these habitats.

TABLE 1

A Breakdown of the various Types of habitats sampled at each Site

Hard substrata (epifauna)	natural	intertidal	marine	sheltered	Murrumbulga Pt
				exposed	Munganno Pt
			estuarine (oysters)		Nullica River Fisheries Creek
		subtidal		sheltered	Murrumbulga Pt
				exposed	Munganno Pt
	artificial — wharf piles, breakwater				Munganno Pt Quarantine Bay
Soft substrata (infauna)	marine	shallow	*Posidonia* (seagrass beds)		Quarantine Bay
		deep (10-20m) — pipe dredge sampling marine sand			
	estuarine	lagoon, *Ruppia* (seagrass beds)			Fisheries Creek
		tidal, *Zostera* (seagrass beds)			Nullica River Curalo Lagoon Shadracks Creek
		saltmarsh			Fisheries Creek Curalo Lagoon

METHODS

The habitats sampled in Twofold Bay (Table 1) were: —

a. Fouling communities on wharfs and piles.
b. Seagrass communities at the mouth of rivers and creeks.
c. Soft bottom communities and intertidal encrusting fauna in shallow estuarine areas.
d. Intertidal rocks around the loading wharf at the woodchip mill.
e. Saltmarsh areas.

No attempt was made to sample the pelagic or planktonic communities within the Bay.

Fig. 1 indicates the location of each of the sampling sites. Details of sampling and the number of samples collected in each habitat are given in Table 2. A variety of qualitative collecting techniques were used to sample the fauna, although in the Appendix some indication of abundance is given for each species.

Details of collection methods appear in Hutchings *et al.* (1986a, b).

TABLE 2

Details of Times of Sampling at each Site and the Number of Samples collected in each Habitat, during each Collection Period
Unit of collection = 36cm x 44cm plastic bag
Variation between months in collection unit number caused by bad weather and time available for collection

SAMPLE REPLICATES		COLLECTION UNITS					
SITES	YEAR	1984		1985			
	MONTH	SEPT	DEC	MAR	JUN	SEPT	DEC
Munganno Point							
Intertidal rock platform		3	2	2	3	3	4
Subtidal rock platform		3	1	1	2	1	2
Wharf piles		3	2	3	3	3	5
Airlift sediment		1	1	1	—	—	— (a)
Fisheries Creek							
Intertidal rocks		—	1	1	1	1	1
Sand sievings (intertidal)*		6	6	6	6	6	6
Mud sievings (intertidal)*		6	6	6	6	6	6
Mud sievings, *Ruppia**		6	6	6	6	6	6
Saltmarsh		6	1	1	1	1	1
Nullica River							
Sand sievings (intertidal)*		—	6	6	6	6	6
Mud sievings (intertidal)*		6	6	6	6	6	6
Mud sievings, *Zostera**		6	6	6	6	6	6
Intertidal rocks		2	1	2	1	1	2
Shadracks Creek							
Mud sievings, *Zostera**		6	6	6	6	6	6
Sand sievings (intertidal)*		6	—	—	—	—	— (a)
Murrumbulga Point							
Intertidal rock platform		2	2	3	3	3	3
Subtidal rock platform		5	2	3	3	3	2
Quarantine Bay							
Airlift sediment (*Posidonia*)		4	4	4	4	4	4
Amphipod trap, wharf		1	—	1	1	1	1
Curalo Lagoon							
Sand sieving, *Zostera**		6	6	6	6	6	6
Saltmarsh		1	1	1	1	1	1
Total		79	66	71	71	70	74

* Hand corer used.
(a) Discontinued.

On one occasion, permission was given by the shipping authorities to collect the accumulated sediment in the bottom of the ballast water tanks.

Salinity was measured during each collecting period for the estuarine areas sampled.

a. Description of Sampling Sites and Salinity Regimes

1. *Curalo Lagoon*

A shallow brackish water lagoon behind the most northern beach in Twofold Bay. It was closed to the sea in July 1984 for a short period and during this time the lagoon was virtually fresh and the bar was breached between July and September 1984. The lagoon then remained open to the sea for the rest of the survey and the salinity ranged for 20-32°/oo, with an average of 26°/oo. *Zostera* seagrass beds were present near the entrance; they replaced *Ruppia* seagrass beds present before the salinity increased. An extensive saltmarsh occurs on the eastern margin.

2. *Murrumbulga Point*

A south-east facing sheltered rocky shore with the intertidal rock platform approximately 15-20m wide, which has been eroded flat, with scattered rubble, boulders and sand occurring at the north-eastern end. Zonation is not as apparent as at Munganno Point, described below, because of its more sheltered nature, gentle slope and the presence of numerous tidal pools.

The subtidal rock 'platform' is boulder-strewn and uneven, extending gradually to a depth of 9m. The boulders have a cover of kelp and other algae, while the crevices are dominated by sea urchins and encrusting red calcareous algae.

3. *Quarantine Bay*

This bay is protected from heavy seas by a breakwater. Patchy *Posidonia* seagrass beds begin at approximately 2m depth between the rocks and sand. Encrusting and cryptic fauna were also collected from these rocks. The pylons of the recreational/public boating wharf and the intertidal breakwater wall were examined.

4. *Shadracks Creek*

A brackish tidal creek with sandy banks and *Zostera* seagrass growing on a rubble covered mud bottom. It forms a small lagoon behind Legges Beach. It had an average salinity of 14.5°/oo (range 0-27°/oo) and was closed in March, 1985, and remained closed for the rest of the sampling period.

5. *Nullica River*

The estuary has extensive intertidal mud and sand flats. *Zostera* seagrass grows in the channel and tide pools and oysters cover the intertidal rocks. It was always open to the sea at times of sampling with an average salinity of 21.7°/oo (range 11-30°/oo).

6. *Fisheries Creek*

A brackish tidal creek with intertidal mud and sand flats, oyster covered rocks, and the seagrasses *Zostera* and *Ruppia* growing in the deeper back waters. Saltmarshes are present along the bank.

The creek showed an average salinity of 29.8°/oo (range of 20-36°/oo), with salinity falling steeply from the mouth to the seagrass beds, a distance of approximately 500m. The creek was closed to the sea in March 1985 and in full flood in December later that year.

7. *Munganno Point*

A north-west facing exposed rocky shore with the intertidal rock platform approximately 4m wide, backed by a small cliff. The platform varies from a steeply sloping rock face to loose piled rubble with a few tide pools. There is some evidence of zonation. The lower zone is dominated by cunjevoi (*Pyura stolonifera* (Heller)) and mat-forming weed. The upper zone is dominated by serpulid worms (*Galeolaria caespitosa* Savigny) and barnacles. The subtidal rock platform is a tiered 'patchy' outcrop of rocks which extends down to sand at approximately 6m depth. The rocks support a healthy cover of kelp (*Ecklonia radiata* (C.Ag.) J.Ag).

The wharf at Munganno Point extends from the shore for 244m, with maximum water depth 15m. The pylons are constructed of concrete-encased steel. Pylons close to the shore are thickly encrusted with calcareous serpulid worm tubes intertidally, whilst supporting a heavy growth of tunicates, sponges and kelp for their entire length below the low water mark.

RESULTS

In the Appendix the macrobenthic fauna collected at each locality is given, together with an indication of abundance and frequency. Many of the polychaetes and small crustaceans have been identified only to the generic level, as they represent either new species or new records for the area. Representatives of each taxon have been lodged at the Australian Museum and assigned registration numbers to facilitate further identification or confirmation.

The following species have been introduced and are non-indigenous to the bay: *Styela plicata* (Ascidian); *Polycera capensis*, *Theba pisana* and *Crassostrea gigas* (Molluscs); *Notomegabalanus algicola*, *Carcinus maenas* and *Eurylana arcuata* (Crustaceans). Each of these is discussed in detail below.

Styela plicata (Lesueur)

This ascidean or sea squirt has long been known to occur on Australian shores. We recorded it from the subtidal rocks amongst the *Posidonia* seagrass in Quarantine Bay. It has a wide distribution within Australia and is found in many ports of the world.

Recent analysis of the biogeography of this species has indicated that it is non-indigenous to Australia (Kott, 1985). *Styela plicata* is a recognized fouling organism and is likely to have been introduced to Australia attached to ships' hulls. The earliest Australian records date from 1878.

The origin of the Twofold Bay colony is unknown. It may have resulted from the spread of populations already established in Australia or as a direct import from overseas shipping. This could have occurred at any time during the 150 years that the port of Twofold Bay has existed (Matthews, 1947).

Theba pisana (Muller)

This salt-tolerant terrestrial snail was collected from the terrestrial margins of the saltmarsh at Curalo Lagoon. It is recognized as a pest of agricultural crops and gardens (Smith and Kershaw, 1979).

Baker (1986) has reviewed the introduction and spread of *T. pisana* in Australia. It first appeared in South Australia prior to 1928. It is now widely distributed over most of southern Australia but appears to favour a mediterranean-type climate. Its previous distribution includes Europe, the Mediterranean, North Africa, Atlantic Isles and British Isles. It has also been introduced to North America and South Africa.

The mode of introduction into Australia is not known, but it may have been brought to Australia as a food item by Italian migrants (P. Colman, pers. comm.).

Crassostrea gigas (Thunberg)

The Pacific oyster was recorded, in small numbers, at Twofold Bay on the intertidal rocks at the mouth of the Nullica River. This is the first record of occurrence in Twofold Bay (T. Mundy, pers. comm.).

Shipments of the Pacific oyster were made from Japan in 1947-8 to establish populations in southern Tasmania (Thomson, 1952). In 1955, adult Pacific oysters from Tasmania were transported to Mallacoota, Victoria, just south of Twofold Bay. By 1958 a quarter of the population was still alive, but no spatfall was observed during this time (Thomson, 1959).

Wolf and Medcof (1973-4) documented the distribution of *Crassostrea gigas* in New South Wales. They provide an accurate documentation of all the Australian introductions and subsequent dispersal of stock. Although they did not record the species from Twofold Bay, the oyster was recorded from Pambula (1967) and Merimbula (1973) just to the north. Subsequent papers (Medcof and Wolf 1975; Holliday and Nell, 1985; Coleman, 1986) have further examined the expansion of the range of *Crassostrea gigas* and discuss the problems this oyster has caused in the N.S.W. oyster industry which has traditionally been based on the Sydney rock oyster *Saccostrea commercialis*. A breeding population of *C. gigas* has established itself in Port Stephens, N.S.W. (Holliday and Nell, 1985).

The Pacific oyster is providing a case study of the effects of a 'pest' on an established fishery.

Polycera capensis (Quoy and Gaimard)

The first Australian records of this opisthobranch mollusc date from 1927, the animals being collected from Sydney Harbour and described by Allan (1932) as a new species *Polycera conspicua*.

Thompson (1975) reported that the species described by Allan (1932) had been synonymized with *Polycera capensis* (Quoy and Gaimard) a species commonly found in, and first described from, South Africa. Thompson (1975) also noted that further specimens had been taken from Sydney Harbour and Botany Bay, N.S.W., where the species was at least seasonally abundant.

Burn (1978) gives the Australian distribution of *P. capensis* as the area between Broken Bay and Kiama, N.S.W.

Willan and Coleman (1984) repeated the Australian distribution given by Burn (1978) and state '*P. capensis* was probably introduced to Australia by shipping'.

A single specimen was collected in December 1985 by us from Twofold Bay, at the subtidal rocks Munganno Point, adjacent to the woodchip loading wharf. Specimens were also taken from this area by Rudman (pers. comm.) in March, 1986.

The evidence to date suggests that *P. capensis* has been introduced into Australia from South Africa, by ship fouling. It may have been introduced to Twofold Bay either directly in this manner or from the dispersal of populations established in other Australian ports.

Polycera capensis was not recorded by us as an introduction to Twofold Bay in our original report (Hutchings *et al.*, 1986b) as the literature relating to it has only recently been brought to our attention.

Notomegabalanus algicola (Pilsbry)

This barnacle was originally described from South Africa and was first noted in Australia by Pope in 1943 (see Allen, 1953). It seems likely that the first introduction occurred in the Sydney region, although the barnacle may have been introduced into New South Wales on several occasions.

Allen (1953) records this barnacle from Eden to Port Stephens and suggests that it was transported to Australia as a fouling species on the bottom of ships. Allen states that during the late 1940s to early 1950s it rapidly increased in numbers and became one of the most common sublittoral barnacles on the open coast. The record of this barnacle from Twofold Bay is therefore not surprising. It was found to be very common on the intertidal rocks and wharf piles of Munganno Point.

Carcinus maenas (Linnaeus)

This species, also known as the European swimming crab, was first recorded from Australia by Fulton and Grant (1900; 1901) from Port Phillip Bay, Victoria. They suggest it was introduced amongst the dense fouling growth on the bottoms of wooden ships and that the young crabs could easily live amongst this growth during the long sea voyage from Europe.

This crab has since been recorded from Westernport Bay to Mallacoota (Allen, 1953), and Healy and Yaldwyn (1970) recorded it as quite abundant on parts of the Victorian coastline. Day and Hutchings (1984) tentatively recorded it from Merimbula, New South Wales, and specimens with collection localities in the vicinity of Narooma, New South Wales, are held at the Australian Museum. We have found it commonly around Twofold Bay, amongst intertidal rocks as well as intertidal mud. Our survey thus confirms the continued extension of *C. maenas* populations to the north. Recent introductions of *C. maenas* have also been reported in South Australia, and a single specimen has been found in Western Australia (Zeidler, 1978; Rosenzweig, 1984).

To date, no information is available on the impact of this introduced species on our native populations. Overseas experience indicates that such an 'aggressive predator' constitutes a potential threat to native marine fauna (Joska and Branch, 1986).

Eurylana arcuata (Hale)

This cirolanid isopod is well known only from New Zealand and Chile, South America. It is believed to have been a recently-introduced species in San Francisco Bay, U.S.A. (Bowman *et al.*, 1981). Bowman *et al.* suggest the isopod could have been introduced to San Francisco Bay in this case either in fouling, such as that found on propeller-shaft housing, or via ballast water. They gave three localities in Australia where this isopod has been previously reported (Port Jackson and Broughton Island, New South Wales and Port Willunga, South Australia) and suggested that it may have been introduced at these points. Bruce (1986) has recorded a single specimen from Newcastle harbour and Day and Hutchings (1984) recorded the species tentatively from Pambula and Merimbula. At Twofold Bay, the species occurred on the intertidal rock platform at Murrumbulga and offshore in deep water sediments.

This disjunct distribution within Australia, associated with port facilities, and the fact that *Eurylana arcuata* is not recognized as an active swimmer (N. Bruce, pers. comm.), indicates that it may have been introduced on several different occasions at different localities.

Sediment in ballast water tanks

The sediment collected from the bottom of the empty ballast water tanks contained one juvenile crab and 60 copepods. The crab was identified as *Charybdis* cf. *feriatus* which has an Indo-Pacific distribution from Japan and East Asia to the east coast of Africa and south to Victoria, Australia. No specimens of this species were recorded during the survey and we cannot be certain that the crab was alive when the mud was collected although it was well preserved and its presence in the sediment confirms the findings of Williams *et al.* (1988).

The 60 copepods present in the mud have not been identified further. However the material has been deposited in the Australian Museum.

DISCUSSION

The benthic macrofauna of Twofold Bay is a rich and diverse one, with over 570 taxa collected. This number includes 13 species of demersal fish which normally inhabit the seagrass beds which were sampled for their benthic invertebrates. This level of richness appears high for southern New South Wales and exceeds the 246 invertebrate species identified at nearby Merimbula (Day and Hutchings, 1984). There is some overlap in species composition in the comparable habitats sampled at these two localities.

Of the seven marine species recorded during this survey as non-indigenous to Twofold Bay, two may have been introduced via ballast water, *Eurylana arcuata* and *Crassostrea gigas*. The remaining species, with the exception of *Theba pisana*, were probably introduced as fouling organisms. The influence of these seven introduced species on the ecology of the indigenous marine life in the bay is not known. To date only the Pacific oyster *Crassostrea gigas* has been recognized as posing a possible commercial threat to fisheries and this is a state wide problem not one restricted to Twofold Bay. The spread of *Carcinus maenas* along the southern and south-eastern Australian coastline and possibly into Western Australia may warrant further studies including ones to assess the impact this species has on the local fauna.

Joska and Branch (1986) describe *Carcinus maenas* as an 'aggressive predator' where 'the great strength of its nippers and its aggressive, non-selective predatory habits have made it a pest in at least one of its adopted habitats'. They report *C. maenas* feeding on the clam-beds on the New England coast of the U.S.A.

This survey provides a basic inventory of the macrofauna of shallow intertidal and subtidal benthic communities in Twofold Bay and should allow any subsequent introductions to be identified and the timing of the introduction to be assessed.

To date we believe that the evidence for introductions via ballast water into Twofold Bay are only tentative and the effect on the native fauna not well documented except in the case of *Crassostrea gigas*. Suggestions made by Paxton and Hoese (1985) and Williams *et al.* (1988), that all ballast water being discharged into Australian ports be treated in order to kill any living organisms before the water is discharged, are at this stage we believe premature. The problems of introducing the necessary legislation which would involve co-operation between several countries, and the enforcing of any such legislation are such that far more documentation of introductions via ballast water and their impact on the native fauna is needed for their justification. Carlton (1985, 1987) in a recent review of ballast water introductions summarizes those attributed to ballast water but in many cases the data substantiating such a mechanism of introduction is fairly tenuous. Instead of pursuing costly legislation to sterilize ballast water, baseline surveys of the fauna and flora of those Australian ports which regularly receive ballast water (especially those which receive ballast water from ports subjected to similar water temperature regimes as those in the Australian port) should be conducted.

Such a monitoring programme and the identification of any introduction and documentation of the impact these introductions are having on the natural fauna will provide the necessary data which would be necessary before any legislative programme could even be considered and drawn up and enforced.

ACKNOWLEDGEMENTS

The study was funded by a Fishing Industry Research Trust Account grant (84-49). The work would not have been possible without the assistance of the following people: E. A. Bamber, L. M. Walker, A. C. Paul, A. L. Reid, S. J. Perry and P. L. Albertson of the Australian Museum who helped in the field; P. Albertson, L. Albertson, L. Matthews and D. Winn of the Australian Museum who helped in the laboratory; P. Went (General Manager) and G. Hodkinson (Shipping Manager) of Harris-Daishowa (Aust.) Pty. Ltd. for access to sample the Munganno Point area and for helpful co-operation shown at all times; D. Laffam (Customs Office at Eden) for his help in organizing the collection of ballast-tank mud from a Malayasian carrier in September 1984. We are also grateful to the following people for their taxonomic help: Dr H. Paxton, Dr H. ten Hove, Dr K. Fauchauld, Dr P. Knight-Jones, C. Glasby, C. Watson-Russell, L. M. Walker and S. J. Perry (Polychaetes); Dr J. Lowry, Dr N. Bruce, Dr G. Poore, Dr A. Myers, D. Jones, H. Stoddart, P. Berents, H. Tranter, R. Springthorpe, A. Murray, M. Drummond and Dr C. Pregenzer (Crustacea); Dr W. Ponder, Dr W. Rudman, I. Loch, P. Colman, J. Kerslake, B. Jenkins and T. Cochran (Molluscs); Dr W. Rudman kindly provided us with his unpublished list of Opisthobranchs from Twofold Bay, Dr F. Rowe (Echinoderms and Urochordates); Dr D. Hoese, D. Rennis and S. Reader (fish). Our special thanks go to Dr A. Jones of the Australian Museum for his advice on sampling strategies, Dr N. Tate for the loan of hand corers, A. Reid for the artwork and to P. Dempsey for typing the manuscript. T. Mundy (Eden's Fishing Inspector) and R. J. Williams are specially acknowledged for their continued interest, constructive criticism and general assistance throughout the course of the study.

References

ALLEN, J. K., 1932. — Australian Nudibranchs. *Aust. Zool.* 7(2): 87-105.

ALLEN, F. E., 1953. — Distribution of marine invertebrates by ships. *Aust. J. mar. Freshwater Res.* 4(2): 307-316.

BAKER, G. H., 1986. — The Biology and Control of White Snails (Mollusca: Helicidae), Introduced Pests in Australia. C.S.I.R.O. Australia. Division of Entomology Technical Paper No. 25. 31pp.

BOWMAN, T. E., BRUCE, N. L. and STANDING, J. D., 1981. — Recent introduction of the cirolanid isopod crustacean *Cirolana arcuata* into San Francisco Bay. *J. Crust. Biol.* 1(4): 545-557.

BRUCE, N. L., 1986. — Cirolanidae (Crustacea: Isopoda) of Australia. *Rec. Aust. Mus. Suppl.* 6: 1-239.

BURN, R., 1978. — A new record of *Thecacera pennigera* (Montagu, 1815). Opisthobranchia: Polyceridae) from New South Wales. *J. Malac. Soc. Aust.* 4(1-2): 22.

CARLTON, J. T., 1985. — Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. *Oceanogr. Mar. Biol. Ann. Rev.* 23: 313-371.

——, 1987. — Patterns of transoceanic marine biological invasion in the Pacific Ocean. *Bull. Mar. Sci.* 41(2): 452-465.

COLEMAN, N., 1986. — A review of introductions of the Pacific oyster (*Crassostrea gigas*) around the world and a discussion of the possible ecological consequences of introducing the species into Victoria, Australia. Marine Science Laboratories, Technical Report No. 56. 39pp.

DAY, J. H., and HUTCHINGS, P. A., 1984. — Descriptive notes on the fauna and flora of Merimbula, Pambula and Back Lakes, New South Wales. *Aust. Zool.* 21(3): 269-289.

FRIESE, U., 1973. — Another Japanese Goby in Australian waters; what next? *Koolewong. Proc. Roy. Zool. Soc. N.S.W.* 2: 5-7.

FULTON, S. W., and GRANT, F. E., 1900. — Note on the occurrence of the European crab, *Carcinus maenas*, Leach, in Port Phillip. *Victorian Nat.* 17(8): 147-148.

——, 1901. — Some little known Victorian Decapod Crustacea with Description of a New Species. *Proc. Roy. Soc. Vict.* 14(2): 55-64.

HEALY, A., and YALDWYN, J., 1970. — *Australian Crustaceans in Colour.* Sydney: Reed.

HOLLIDAY, J. E., and NELL, J. A., 1985. — Concern over Pacific oyster in Port Stephens. *Aust. Fish.* 44(11): 29-31.

HUTCHINGS, P. A., van der VELDE, J. T., and KEABLE, S. J., 1986a. — Colonisation of New South Wales by non-indigenous marine species. Baseline studies at Twofold Bay, New South Wales. Unpublished final report to the Fisheries Industry Research Committee. FIRTA 84-89. 71pp.

——, 1986b. — Colonisation of N.S.W. by foreign marine species. *Aust. Fish.* 45(4): 40-42.

JOSKA, M. A., and BRANCH, G., 1986. — The European shore-crab. Another alien invader? *Afr. Wildl.* 40(2): 63-65.

KOTT, P., 1985. — The Australian Ascidiacea Part 1. Phlebobranchia and Stolidobranchia. *Mem. Qld Mus.* 23: 1-440.

MATTHEWS, L. J., 1947. — Eden, Twofold Bay. Its Rise, Decline and Return to Prosperity. *Port of Sydney Journal* 1(3): 89-92.

MEDCOF, J. C., 1975. — Living marine animals in a ship's ballast water. *Proc. natl Shellfish. Ass.* 65: 54-55.

——, and WOLF, P. H., 1975. — Spread of Pacific oyster worries New South Wales culturists. *Aust. Fish.* 34(7): 32-38.

PAXTON, J. R., and HOESE, D. F., 1985. — The Japanese Sea Bass, *Lateolabrax japonicus* (Pisces, Percichthyidae), an Apparent Marine Introduction into Eastern Australia. *Jap. J. Ichthyol.* 31(4): 369-372.

ROSENZWEIG, P. A., 1984. — A range extension for the European shore crab *Carcinus maenas* (Linn, 1758) in South Australia. *Sth Aust. Nat.* 59(1): 18-19.

SMITH, B. J., and KERSHAW, R. C., 1979. — *Field Guide to the Non-Marine Molluscs of South Eastern Australia.* Canberra: Australian National University Press.

THOMPSON, T. E., 1975. — Dorid nudibranchs from eastern Australia (Gastropoda, Opisthobranchia). *J. Zool. Lond.* 176: 477-517.

THOMSON, J. M., 1952. — The acclimatization and growth of the Pacific oyster (*Gryphaea gigas*) in Australia. *Aust. J. Mar. Freshwater Res.* 3(1): 64-73.

——, 1959. — The naturalization of the Pacific oyster in Australia. *Aust. J. Mar. Freshwater Res.* 10(2): 144-149.

WILLAN, R. C., and COLEMAN, N., 1984. — *Nudibranchs of Australasia.* Sydney: Australian Marine Photographic Index.

WILLIAMS, R. J., van der WAL, E. J., and KELLY, J., 1988. — Ballast water as a possible vector for the transport of non-indigenous marine species. *Estuarine, Coastal, Shelf Science* 26: 409-420.

WOLF, P. H., and MEDCOF, J. C., 1973-4. — Be on your guard against the Pacific oyster. *The Fisherman* 4(10) 3-5, 24-25.

ZEIDLER, W., 1978. — Note on the occurrence of the European shore crab *Carcinus maenas* (Linn., 1758) in Australia. *Sth Aust. Nat.* 53(1): 11-12.

APPENDIX

INVENTORY OF MARINE FAUNA COLLECTED FROM TWOFOLD BAY

(In alphabetical order within the major taxonomic groupings)

The *frequency* refers to the rate of recurrence or number of collections in which it was found:

Occasionally (o)	$0 < x < 2$
Usually (u)	$2 < x < 4$
Regularly (r)	$4 < x < 6$

where x represents the number of collections.

The *abundancy* was a subjective measure of how plentiful the species was, based on the total numbers collected in that group. As the project was essentially a qualitative exercise sampling method and effort varied. Thus comparisons between groups proved difficult and a sliding scale was adopted. For example:

Few (f) =	not many, small in number for polychaetes	$x < 20$
	molluscs	$x < 20$
	(peracarid (small) crustacea	$x < 50$
	other crustacea	$x < 20$
Abundant (a) =	plentiful, polychaetes	$20 < x < 50$
	molluscs	$20 < x < 40$
	(peracarid crustacea	$50 < x < 100$
	other crustacea	$20 < x < 40$
Numerous (n) =	consisting of a great number, polychaetes	$x > 50$
	molluscs	$x > 40$
	peracarid crustacea	$x > 100$
	other crustacea	$x > 40$

where x represents the number of specimens.

The *sites* are Curalo Lagoon — 1, Murrumbulga Point — 2, Quarantine Bay — 3, Shadracks Creek — 4, Nullica River estuary 5, Fisheries Creek — 6, Munganno Point — 7, Reconnaissance trip (12-13/7/84) — 8, Deepwater benthic sampling (20-22/2/85) — 9.

CLASSIFICATION & DESIGNATION	FREQUENCY/ ABUNDANCY	FOUND AT SITES	REGISTRATION NOS
PHYLUM: COELENTERATA			
Phlyctenactis tuberculosa (Quoy & Gaimard)	o/f	2,7	G15228
PHYLUM: PLATYHELMINTHES			
CLASS: TURBELLARIA:			
Acoela spp.	u/a	2,3,7	W201435-6
PHYLUM: NEMERTINEA			
Nemertean ?sp.1	r/n	1,2,3,5,6,7	W201433-4
Nemertean ?sp.2	u/a	2,3,5,7	W201431-2
Nemertean ?sp.3	r/a	2,3,5,7	W201429-30
Nemertean ?sp.4	r/a	2,6	W201427-8
Nemertean ?sp.5	o/f	4,7	W201426
Nemertean ?sp.6	o/f	7	W201425
PHYLUM: ANNELIDA			
CLASS: POLYCHAETA			
ORDER: ORBINIIDA			
FAMILY: ORBINIIDAE			
Leitoscoloplos normalis Day	u/a	1,2,3,4,5,6	W201397
Scoloplos (Scoloplos) cylindrifer Ehlers	o/f	1	W201400
Scoloplos (Scoloplos) novaehollandiae (Kinberg)	o/f	1	W201399
Scoloplos (Scoloplos) simplex (Hutchings)	u/f	1,2,3,4,6	W201398
FAMILY: PARAONIDAE	o/f	5	W202618
ORDER: SPIONIDA			
FAMILY: SPIONIDAE			
Aonides oxycephela (Sars)	f	3,5	W201392
Australospio trifida Blake & Kudenov	f	7	W201396
Boccardia chilensis Blake & Woodwick	f	2,5,7	W201391
Boccardiella sp.	f	2	W201388
Carazziella victoriensis Blake & Kudenov	f	3	W201390
?*Laonice* sp.	f	2,5,7	W201393
Malacoceros sp.	f	6	W201387
Polydora socialis (Schmarda)	f	3,7	W201389
Polydora cf. *woodwicki*	f	5	W201394
Polydora sp.	f	3,5	W201385
Prionospio cirrifera Wiren	f	2,3	W201395
Prionospio cf. *cirrifera*	f	4,5	W201386
Prionospio multipinnulata Blake & Kudenov	f	2,3,7	W201384
Spio pacifica Blake & Kudenov	f	6	W201383
FAMILY: MAGELONIDAE	o/f	5	W201382
SUB ORDER: CHAETOPTERIFORMIA			
FAMILY: CHAETOPTERIDAE			
Mesochaetopterus sp.	o/f	7	W199764
SUB ORDER: CIRRATULIFORMIA			
FAMILY: CIRRATULIDAE			
Cirriformia capensis (Schmarda)	f	2,7	W202616
Cirriformia filigera (delle Chiaje)	f	2,5	W202617
Dodecaceria sp.	o/f	2	W199748
ORDER: CAPITELLIDA			
FAMILY: CAPITELLIDAE			
Barantolla lepte Hutchings	o/f	5	W201381
Capitella 'capitata' (Fabricius)	o/f	1	W20138
Leiocapitella sp.	o/f	7	W201378
Notomastus torquatus Hutchings & Rainer	o/f	5	W201379

Appendix cont'd.

FAMILY: MALDANIDAE			
Axiothella sp.	u/a	1,2,3,5	W199732-41
Euclymene trinalis Hutchings	o/f	3	W199742
ORDER: OPHELIDA			
FAMILY: OPHELIIDAE	u/f	7	W202619
FAMILY: SCALIBREGMIDAE	o/f	2,3	W201412
ORDER: PHYLLODOCIDA			
SUB ORDER: PHYLLODOCIFORMIA			
FAMILY: PHYLLODOCIDAE			
Anaitides longipes (Kinberg)	r/a	2,3	
Eumida cf. *sanguinea*	r/a	2,7	W202472
Phyllodoce novaehollandiae Kinberg	r/a	1,3,4,5,6	entire
Phyllodoce sp.1	u/f	6,7	family
Phyllodocid sp.1	o/f	2	currently
Phyllodocid sp.2	o/f	7	being
Phyllodocid sp.3	o/f	7	revised
SUB ORDER: APHRODITIFORMIA			
FAMILY: POLYNOIDAE			
Harmothoe sp.1	u/f	2,3,7	W201418
Harmothoe sp.2	r/a	2,3,5	W201417
Lepidasthenia sp.	o/f	7	W201422
Lepidonotus carinulatus Grube	o/f	5	W201421
Lepidonotus melanogrammus Haswell	o/f	7	W201420
Lepidonotus n.sp.1	r/a	2,5,6,7	W201416
Lepidonotus n.sp.2	r/a	2,3,7	W201415
Lepidonotus n.sp.3	r/a	2,7	W201414
Lepidonotus n.sp.4	o/f	2	W201419
FAMILY: SIGALIONIDAE			
Psammolyce cf. *antipoda*	u/f	3	W201413
Sigalion bandaeensis Horst	o/f	5,6	W199763
FAMILY: CHRYSOPETALIDAE			
Chrysopetalum sp.1	r/a	2,7	W199721-31
SUB ORDER: NEREIDIFORMIA			
FAMILY: HESIONIDAE			
Podarke angustifrons (Grube)	r/a	2,3,5,7	W201374
FAMILY: SYLLIDAE			
Autolytus sp.1	u/f	7	W201364
Autolytus sp.2	o/f	7	W201365
Autolytus sp.3	o/f	7	W201366
Autolytus sp.4	o/f	2	W201367
Syllid ?sp.1	r/n	1,2,3,5,6,7	W201368
Syllid ?sp.2	r/n	1,2,7	W201369
Syllid ?sp.3	r/a	2,3,7	W201370
Syllid ?sp.4	o/f	4,7	W201371
Syllid ?sp.5	o/f	2,7	W201372
Syllid ?sp.6	u/f	2,7	W201373
FAMILY: NEREIDIDAE			
Australonereis ehlersi (Augener)	r/a	1,2,5,6	W201361
Ceratonereis aequisetis Augener	r/n	1,2,3,4,5,6,7	W201362
Nereis maxillodentata Hutchings & Turvey	o/f	7	W202521
Nereis cf. *triangularis*	o/f	7	W202607
Perinereis amblyodonta (Schmarda)	r/n	1,2,3,4,5,6,7	W201363
Platynereis dumerilii antipoda Hartman	o/f	2,3,5,7	W202610
SUB ORDER: GLYCERIFORMIA			
FAMILY: GLYCERIDAE			
Glycera tridactyla Schmarda	o/f	3,9	W199743-7

Appendix cont'd.

FAMILY: NEPHTYIDAE			
Nephtys australiensis Fauchald	r/n	1,3,4,5,6	W200238-337
ORDER: AMPHINOMIDA			
FAMILY: AMPHINOMIDAE			
Euphrosine n.sp.	o/f	7	W199762
ORDER: EUNICIDA			
FAMILY: EUNICIDAE			
Eunice aphroditois (Pallas)	r/a	2,7	W201411
Eunice cf. *australis*	r/a	2,7	W201410
Eunice torresiensis McIntosh	o/f	7	W201409
Eunice tridentata Ehlers	o/f	2	W201408
Eunice tubifex Crossland	o/f	7	W201407
Marphysa sanguinea (Montagu)	o/f	2	W201406
Nematonereis unicornis (Grube)	u/f	2,7	W199804-5
Palola sp.1	o/f	7	W201405
FAMILY: ONUPHIDAE			
Diopatra dentata Kinberg	r/a	2,7	W200191-202
FAMILY: LUMBRINEREIDAE			
Augeneria verdis Hutchings & Murray	o/f	3,7	W201403
Lumbineris latreilli Audouin & Milne Edwards	o/f	5	W201402
FAMILY: ARABELLIDAE			
Arabella iricolor iricolor (Montagu)	o/f	2,3,7	W201401
Arabella n.sp.1	r/n	1,2,3,5,6,7	W198896-976
FAMILY: LYSARETIDAE			
Lysidice cf. *collaris*	r/a	2,3,7	W19773-802
Lysidice ninetta Audouin & Milne Edwards	o/f	7	W199803
?*Lysidice* sp.	o/f	2	W201404
FAMILY: DORVILLEIDAE			
Dorvillea australiensis (McIntosh)	o/f	2,3,7	W199751-4
Protodorvillea sp.	o/f	6,7	W199749-50
Schistomeringos loveni (Kinberg)	u/f	2,3,5	W199755-9
ORDER: OWENIIDA			
FAMILY: OWENIIDAE			
Owenia fusiformis delle Chiaje	r/n	1,3,4,5,6	W200203-34
ORDER: TEREBELLIDA			
FAMILY: SABELLARIIDAE			
Idanthyrsus pennatus (Peters)	u/a	2,7	W199879-95
FAMILY: AMPHARETIDAE			
Isolda pulchella Muller	u/a	2,7	W199760-1
FAMILY: TEREBELLIDAE			
Lanassa ocellata Hutchings & Glasby	o/f	2	
Lanice bidewa Hutchings & Glasby	o/f	9	W201375
Longicarpus modesta Hutchings & Murray	u/a	2,7	W200388-97
Nicolea amnis Hutchings & Murray	r/a	2,3,7	W200375-80
Pista australis Hutchings & Glasby	u/f	3,5,7	W200635-7
Pista violacea Hartmann-Schröder	o/f	3	W200906
Reteterebella aloba Hutchings & Glasby	u/f	2,3	W200398
Streblosoma acymatum Hutchings & Rainer	o/f	9	W201377
Terebella pappus Hutchings & Murray	u/a	2,5,7	200404-10
Thelepus boja Hutchings & Glasby	o/f	7	W198918
Thelepus brevicauda Hutchings & Glasby	o/f	7	W201376
Thelepus extensus Hutchings & Glasby	u/a	2,3,5,7	W198916-7
ORDER: SABELLIDA			
FAMILY: SABELLIDAE			
Amphiglena mediterranea (Leydig)	u/f	2,7	W199827-30
Branchiomma nigromaculata (Baird)	r/n	2,3,7	W199831-70

Appendix cont'd.

Megalomma sp.	r/a	2,7	W199812-26
Sabellastarte indica (Savigny)	u/f	2,3,7	W199765-72
FAMILY: SERPULIDAE			
Galeolaria caespitosa Savigny	r/n	2,3,5,6,7	W201358
Hydroides cf. *brachyacantha*	r/a	2,7	W201357
Neovermilia globula Dew	o/f	2,7	W201355
Pomatoceros sp.1	r/a	2,7	W201356
Pomatoceros sp.2	r/n	2,3,7	W201360
Protula sp.1	o/f	7	W201354
Serpula jukesii Baird	u/f	2,3	W201359
Serpula rubens Straughan	u/a	2,3,7	W201352
Serpula sp.1	u/f	2,7	W201353
Spirobranchus tetraceros (Schmarda)	o/f	7	W201351
PHYLUM: MOLLUSCA			
CLASS: POLYPLACOPHORA			
ORDER: NEOLORICATA			
FAMILY: LEPIDOPLEURIDAE			
Parachiton sp.	o/f	7	C148803-4
FAMILY: ISCHNOCHITONIDAE			
Callistochiton antiquus (Reeve)	o/f	7	C150544
Ischnochiton australis Sowerby	r/n	2,3,7	C148821-3
Ischnochiton cariosus (Dall)	r/n	2,3,7	C148813
Ischnochiton elongatus crispus Reeve	r/n	2,3,7	C148824-5
Ischnochiton lentiginosus (Sowerby)	u/f	2	C148820
Ischnochiton smaragdinus (Angas)	u/a	2,3	C148814-6
Ischnochiton versicolor Iredale & Hull	r/a	2,3,7	C148817-9
Ischnochiton sp.1	o/f	2	C148826
Ischnochiton sp.2	o/f	2,7	C148827
FAMILY: MOPALIIDAE			
Plaxiphora albida (Blainville)	r/a	7	C148802
Plaxiphora matthewsi Iredale	u/f	7	C148807-8
FAMILY: SCHIZOCHITONIDAE			
Lorica volvox (Reeve)	o/f	7	C150545
FAMILY: CHITONIDAE			
Chiton jugosus Gould	r/f	2	C148797
Chiton pelliserpentis maugeanus (Iredale & May)	r/n	2,5,6,7	C148798-800
FAMILY: ACANTHOCHITONIDAE			
Acanthochitona pilsbryi (Sykes)	r/n	2,7	C148809-10
Acanthochitona retrojecta (Pilsbry)	r/n	2,7	C148811
Acanthochitona sp.1	u/f	2,7	C148812
Notoplax cf. *rubrostrata*	u/f	2,7	C148805-6
CLASS: BIVALVIA			
ORDER: NUCULOIDA			
FAMILY: NUCULANIDAE			
Nuculana spathula (Hedley)	o/f	9	C150568
Scaeoleda hanleyi (Angas)	r/n	9	C150570
ORDER: SOLEMYOIDA			
FAMILY: SOLEMYIDAE			
Solemya australis (Lamarck)	u/a	2,3	C148522
ORDER: ARCOIDA			
FAMILY: ARCIDAE			
Barbatia pistachia (Lamarck)	u/f	2	C148542
Acar botanica (Hedley)	o/f	2	C148541
FAMILY: GLYCYMERIDIDAE			
Glycymeris flammeus (Reeve)	o/a	8,9	C148794-5

Appendix cont'd.

ORDER: MYTILOIDA			
FAMILY: MYTILIDAE			
Mytilus edulis (Linnaeus)	r/n	2,3,5,6,7	C148548-9
Austromytilus rostratus Dunker	o/f	7	C150549
Trichomya hirsuta (Lamarck)	r/n	2,5,7	C148538-40
Musculus nanus (Dunker)	r/n	7	C148533
Musculus sp.(juv.)	u/n	2,7,9	C148534
Trichomusculus barbatus Reeve	r/n	7	C148537
Modiolus areolatus (Gould)	u/f	7	C148532
Xenostrobus securis (Lamarck)	o/f	2	C150577
ORDER: PTERIOIDA			
FAMILY: PTERIIDAE			
Electroma georgiana (Quoy & Gaimard)	o/f	9	C150558
FAMILY: PULVINITIDAE			
Vulsella vulsella (Linnaeus)	o/f	2,7	C148535
FAMILY: PECTINIDAE			
Mimachlamys asperrimus (Lamarck)	u/f	7	C150563
FAMILY: ANOMIIDAE			
Anomia descripta Iredale	o/f	7	C150548
Anomia ione (Gray)	u/f	3,7	C148530
Monia zealandica (Gray)	o/f	2	C150564
FAMILY: LIMIDAE			
Lima nimbifer (Iredale)	o/f	7	C148536
FAMILY: OSTREIDAE			
Ostraea angasi Sowerby	u/f	5,7	C148793
Crassostrea gigas (Thunberg)	o/f	5	C150556
Saccostrea commercialis (Iredale & Roughley)	r/n	2,5,6,7	C148796
ORDER: VENEROIDA			
FAMILY: LUCINIDAE			
Wallucina assimilis (Angas)	u/f	3	C148523
FAMILY: ERYCINIDAE			
Lasaea australis (Lamarck)	r/n	2,5,6,7	C148545-6
FAMILY: GALEOMMATIDAE			
Ambuscintilla praemium Iredale	r/a	5	C150547
FAMILY: CARDITIDAE			
Cardita excavata Deshayes	o/f	7	C150553
FAMILY: CORDIIDAE			
Acrosterigma cygnorum (Deshayes)	o/f	3	C150546
Fulvia tenuicostata (Lamarck)	o/f	3	C148521
FAMILY: MACTRIDAE			
Spisula trigonella (Lamarck)	o/f	4,5,6	C150572
FAMILY: MESODESMATIDAE			
Mesodesma elongata (Reeve)	o/f	6,9	C148516
FAMILY: SOLENIDAE			
Solen vaginoides (Lamarck)	o/f	9	C150571
FAMILY: TELLINIDAE			
Tellina deltoidalis (Lamarck)	r/n	1,3,4,5,6	C148517
Tellina tenuilirata Sowerby	u/f	9	C150573
Tellina sp.	r/a	3,9	C150574-5
FAMILY: DONACIDAE			
Donax sp. (juv.)	o/f	5,6	C150557
FAMILY: PSAMMOBIIDAE			
Gari sp.	o/f	9	C150559
Sanguinolaria donacioides (Reeve)	o/f	1,6	C148543

Appendix cont'd.

FAMILY: VENERIDAE			
?*Notocallista* sp.	o/f	7	C150567
Eumarcia fumigata (Sowerby)	r/a	1,3,4,5,6	C148525
Venerupis crenata (Lamarck)	r/n	2,5,6,7	C148518
Venerupis fabagella (Deshayes)	u/a	2,3,7	C148519-20
Bassina pachyphylla (Jonas)	o/f	9	C150551
Placamen placidum (Philippi)	o/f	9	C150569
Timoclea cardiodes (Lamarck)	o/f	3	C148524
ORDER: MYOIDA			
FAMILY: CORBULIDAE			
Corbula smithiana Brazier	o/f	5,9	C150554-5
FAMILY: TEREDINIDAE			
Teredo sp.	o/f	2	C150576
Bankia sp.	o/f	1	C150550
FAMILY: HIATELLIDAE			
Hiatella australis (Lamarck)	r/n	7,9	C148531
ORDER: PHOLADOMYOIDA			
FAMILY: LATERNULIDAE			
Laternula creccina Reeve	o/f	9	C150560-1
Laternula cf. *creccina*	o/f	1,5	C148544
FAMILY: MYOCHAMIDAE			
Myadora pandoriformis (Stutchbury)	o/f	9	C150565
CLASS: GASTROPODA			
SUBCLASS: PROSOBRANCHIA			
ORDER: ARCHAEOGASTROPODA			
FAMILY: HALIOTIDAE			
Haliotis ruber (Leach)	u/f	2,7	C148851
FAMILY: FISSURELLIDAE			
Amblychilepas javanicensis (Lamarck)	o/f	7	C150578
Diodora lineata (Sowerby)	o/f	2	C150580
Emarginula sp.	o/f	7	C148850
Scutus antipodes Montfort	r/a	2,3,7	C148848
Scutus sp. (juv.)	u/f	2	C148849
FAMILY: PATELLIDAE			
Cellana tramoserica (Holten)	r/n	2,5,6,7	C148828-9
?*Cellana tramoserica*	o/f	2	C150579
Patella chapmani (Tenison-Woods)	u/f	2,7	C148845-7
Patella peroni (Blainville)	r/a	2,7	C148842-3
FAMILY: ACMAEIDAE			
Notoacmea flammea (Quoy & Gaimard)	u/f	2,7	C148844 C150584
Notoacmea petterdi (Tenison-Woods)	r/n	2,7	C148841
Patelloida alticostata (Angas)	r/n	2,7	C148830-1
Patelloida latistrigata (Angas)	r/a	2,7	C148832-4
Patelloida mimula (Iredale)	r/n	5,6	C148835-7
Patelloida mufria (Hedley)	r/n	2,3,7	C148838-40
FAMILY: TROCHIDAE			
Austrocochlea concamerata (Wood)	r/n	2,7	C148493
Austrocochlea constricta (Lamarck)	r/n	2,5,6,7	C148496-7
Austrocochlea sp. (juv.)	o/f	2,7	C148498
Bankivia fasciata (Menke)	u/n	9	C148390
Cantharidella picturata (A. Adams & Angas)	u/a	2,7	C148374-5
Euriclanculus floridus (Philippi)	r/f	2,7	C148372-3
Eurytrochus strangei (A. Adams)	r/n	2,3,7	C150581
Gena impertusa (Burrow)	r/a	2,3,7	C148369
Granata imbricata (Lamarck)	r/f	2	C148370-1
Herpetopoma aspersa (Philippi)	r/n	2,7	C148367-8

Appendix cont'd.

Kerguelenella stoweai (Verco)	o/f	2	C150582
Leiopyrga lineolaris (Gould)	u/n	9	C148389
Mesoclanculus plebejus (Philippi)	u/a	2	C150583
Montfortula rugosa (Quoy & Gaimard)	r/n	2,7	C148852
Phasianotrochus eximus (Perry)	o/f	2	C148350
Phasianotrochus sp.	u/a	2,3	C150585
Thaliota sp.	u/f	2,7	C148357
Tugali sp.	u/f	2,7	C148861
FAMILY: TURBINIDAE			
Astraea tenforiformis sirius (Gould)	r/a	2,7	C148499
Astralium sp.	o/f	2	C148500
Turbo torquatus (Gmelin)	o/f	2,7	C148502
Turbo undulatus (Solander)	r/a	2,7	C148364-5
FAMILY: NERITIDAE			
Nerita atramentosa (Reeve)	r/n	2,5,7	C148494
ORDER: MESOGASTROPODA			
FAMILY: LITTORINIDAE			
Bembicium auratum (Quoy & Gaimard)	r/n	2,5,6	C148510-1
Bembicium nanum (Lamarck)	r/n	5,7	C148508-9
Nodilittorina pyramidalis (Quoy & Gaimard)	u/a	2,5,7	C148346
Nodilittorina unifasciata (Gray)	r/n	2,5,7	C148345
FAMILY: ASSIMINEIDAE			
Assiminea tasmanica Tenison-Woods	o/f	1	C150586
FAMILY: ARCHITECTONICIDAE			
Philippia lutea (Lamarck;	o/f	7	C148366
FAMILY: VERMETIDAE			
Serpulorbis sipho (Lamarck)	o/f	7	C148507
FAMILY: PLANAXIDAE			
Hinea braziliana Lamarck	o/a	2,7	C15088-9
FAMILY: POTAMIDIDAE			
Pyrazus ebeninus (Bruguiere)	r/f	5,6	C150590
Velacumantus australis (Quoy & Gaimard)	r/n	5,6	C148391-2
FAMILY: CERITHIIDAE			
Bittium sp.	r/n	2,3,7	C148405-7
FAMILY: CREPIDULIDAE			
Crepidula aculeata Gmelin	o/f	2	C150587
FAMILY: NATICIDAE			
Polinices melastomum (Swainson)	o/f	5	C148354
FAMILY: RANELLIDAE			
Cabestana spengleri (Perry)	o/f	8	C148503
Charonia lampax rubicunda (Perry)	o/f	8	C148506
Ranella australasia (Perry)	u/f	2,7	C148504-5
Septa parthenopea (von Salis)	o/f	7	C150591
ORDER: NEOGASTROPODA			
FAMILY: MURICIDAE			
Agnewia tritoniformis (Blainville)	r/a	2,7	C148358
Bedeva hanleyi (Angas)	r/a	2,3,5,6	C1548361
Bedeva sp. (juv.)	o/f	3	C148362
Chicoreus denudatus (Perry)	o/f	7	C148359
Haustrum vinosum (Quoy & Gaimard)	r/a	2	C148355
'Lepsiella' reticulata (Blainville)	u/f	2	C148356
Mesoginella cf. *translucida*	o/f	7	C148387
Mesoginella turbinata (Sowerby)	u/a	9	C148388
Morula marginalba (Blainville)	r/n	2,7	C148495
Thais orbita (Gmelin)	r/n	2,7	C148501

Appendix cont'd.

FAMILY: COLUMBELLIDAE			
Mitrella leucostoma (Gaskoin)	o/f	3	C148377-8
Mitrella lincolnensis (Reeve)	o/f	2,3	C148379-80
Mitrella pulla (Gaskoin)	u/f	2,7	C148381-3
Mitrella sp.	u/f	2,7	C148384-6
FAMILY: BUCCINIDAE			
Cominella lineolata (Lamarck)	r/a	2	C148352-3
FAMILY: NASSARIIDAE			
Nassarius burchardi (Dunker)	r/a	3,4,5,6	C148402
Nassarius cf. *burchardi*	o/f	3	C148401
Nassarius glans particeps (Hedley)	o/f	2,7	C148403
Nassarius pauperatus (Lamarck)	r/n	2,3,7	C148400
Nassarius pauperus (Gould)	o/f	7	C148404
Nassarius sp. (juv.)	u/a	2,3,9	C148399
FAMILY: OLIVIDAE			
Olivella leucozona Adams & Angas	o/f	9	C148376
FAMILY: TURRIDAE			
Guraleus pictus (Adams & Angas)	u/f	3,7	C148363
FAMILY: CONIDAE			
Conus anemone Lamarck	o/f	2	C148351
SUBCLASS: OPISTHOBRANCHIA			
ORDER: BULLOMORPHA			
FAMILY: BULLIDAE			
Bulla quoyii (Gray)	o/f	3	C148360
FAMILY: PHILINIDAE			
Philine cf. *angasi*	o/f	3	C148866
ORDER: ANASPIDEA			
FAMILY: APLYSIDAE			
Aplysia sydneyensis Sowerby	o/f	1	C148512
ORDER: NOTOSPIDEA			
FAMILY: PLEUROBRANCHIDAE			
Pleurobranch sp. 1	o/f	2	C148865
ORDER: NUDIBRANCHIA			
SUBORDER: DORIDACEA			
FAMILY: DORIDIDAE			
Aphelodoris varia (Abraham)	o/f	7	C150593
Dorid Nudibranch sp. 1	o/f	7	C148862
Dorid Nudibranch sp. 2	o/f	7	C148863
FAMILY: CHROMODORIDIDAE			
Ceratosoma amoena (Cheeseman)	o/f	7	C150596
FAMILY: POLYCERIDAE			
Polycera capensis (Quoy & Gaimard)	o/f	7	C150597
SUBORDER: AEOLIDACEA			
FAMILY: GLAUCIDAE			
Austraeolis cacaotica (Stimpson)	o/f	7	C150594
Pteraeolidia ianthina (Angas)	o/f	7	C150598
SUBORDER: ARMINACEA			
FAMILY: JANOLIDAE			
Caldukia affinis (Burn)	o/f	3	C150595
SUBCLASS: PULMONATA			
ORDER: SYSTELLOMMATOPHORA			
FAMILY: ELLOBIIDAE			
Ophicardelus ornatus (Ferussac)	r/n	6	C148393-4
Ophicardelus quoyi (H. & A. Adams)	r/a	6	C148396-7

Appendix Cont'd.

Ophicardelus cf. *quoyi*	o/f	6	C148395
Ophicardelus sulcatus (H. & A. Adams)	u/f	6	C148398
FAMILY: ONCHIDIIDAE			
Onchidella patelloides (Quoy & Gaimard)	r/a	2,5,6	C148859-60
Onchidina australis (Semper)	r/f	6	C148864
ORDER: BASOMMATOPHORA			
FAMILY: SIPHONARIIDAE			
Salinator fragilis (Lamarck)	r/n	1,4,5,6	C148347-8
Salinator solida (von Martens)	r/n	1,6	C148349
Siphonaria denticulata Quoy & Gaimard	r/a	2,7	C148853
Siphonaria diemenensis Quoy & Gaimard	r/n	2,5,7	C148854-5
Siphonaria funiculata Reeve	r/a	2,7	C148856
Siphonaria sp. (juv.)	o/f	7	C148857-8
ORDER: SIGMURETHRA			
Theba pisana (Muller)	o/f	1	C150600
CLASS: SCAPHOPODA			
ORDER: GADILIDA			
FAMILY: SIPHONODENTALIIDAE			
Cadulus acuminatus Tate	u/n	9	C150969
PHYLUM: ARTHROPODA			
CLASS CRUSTACEA			
SUBCLASS: OSTRACODA			
ORDER: MYODOCOPA			
Myodocopa spp.	r/n	2,3,7,9	P36562-83
SUBCLASS: CIRRIPEDIA			
ORDER: THORACICA			
Austrobalanus imperator (Darwin)	f	7	P36114
Austromegabalanus nigrescens (Lamarck)	a	7	P36119
Balanus trigonus Darwin	n	2,7	P36112
Balanus variegatus Darwin	f	6	P36614
Catomerus polymerus (Darwin)	a	2,7	P36122
Chamaesipho columna (Spengler)	n	2,7	P36120
Chthamalus antennatus Darwin	n	2,7	P36124
Elminius covertus Foster	n	2,5,6	P36125
Ibla quadrivalvis Cuvier	f	2,7	P36113
Notomegabalanus algicola (Pilsbry)	n	2,7	P36116-8
Tesseropora rosea Krauss	a	2,7	P36121
Tetraclitella purpurascens (Wood)	n	2,7	P36123
SUBCLASS: MALACOSTRACA			
ORDER: LEPTOSTRACA			
Neballiacean sp.	o/f	9	P36584-7
SUPERORDER: PERACARIDA			
ORDER: MYSIDACEA			
Heteromysis sp.	u/f	2,7	P36617-9
Siriella australis W. M. Tattersall	o/f	7	P36615-6
ORDER: CUMACEA			
Cumacean spp.	r/n	1,3,5,7,9	P36594-613
ORDER: TANAIDACEA			
Tanaidacean spp.	r/n	2,3,7,9	P36525-48
ORDER: ISOPODA			
SUBORDER: GNATHIIDEA			
Gnathia ferox (Haswell)	u/f	3,7	P36588-91
SUBORDER: ANTHURIDEA			
Apanthura drosera Poore & Lew Ton	o/f	9	P36050

Appendix cont'd.

Apanthura isotoma Poore & Lew Ton	u/f	9	P36046-8
Apanthura xanthorrhoea Poore & Lew Ton	r/a	2,3,7	P35640-2 P36154-6
Apanthuretta olearia Poore & Lew Ton	o/f	9	P36049 P36059
Bullowanthura pambula Poore	o/f	9	P36052
Cyathura hakea Poore & Lew Ton	o/f	4	P36593
Haliophasma canale Poore	o/f	9	P36058
Haliophasma sp. 1	o/f	2,7	P36061-2 P36592
Haliophasma sp. 2	o/f	9	P36056-7 P36133-5
Leptanthura diemenensis (Haswell)	r/a	2,3,9	P35648-9 P36053-5 P36170-2
Mesanthura dianella Poore & Lew Ton	u/f	2,3,7	P35643-5 P36149
Paranthura acacia Poore	o/f	9	P36060
Paranthura senecio Poore	r/f	2,7	P35646-7 P36167-9
Ulakanthura marlee Poore	o/f	9	P36051
SUBORDER: FLABELLIFERA			
Amphoroidea angustata Baker	o/f	2	P35957
Cerceis ?obtusa	o/f	2	P36625
Cirolana australiense Hale	r/n	2,3,7,9	P35961 P36146-8
Cirolana victoriae Bruce	o/f	9	P35972
Cilicaea tenuicauda Haswell	o/f	2	P36626
Cilicaeopsis cf. *whiteleggei*	o/f	2	P36627
Cilicaeopsis sp.	o/f	9	P35970
Cymodoce cf. *bidentata*	o/f	9	P35969 P36178
Cymodoce haswelli Harrison & Holdich	u/f	2,7	P36628
Cymodoce spp. (females)	r/n	2,3,7	P35948-9 P35954 P35960 P36145 P36173-4 P36623-4
?*Cymodopsis* sp.	o/f	2	P35955
Cymothoid sp.	o/f	3	P36631
Eurydice ?binda	o/f	7	P36629
Eurydice sp.	o/f	9	P35971
Eurylana arcuata (Hale)	r/f	2,7,9	P35958 P36175-7
Exosphaeroma sp.	o/a	2,7	P35959
Haswellia carnea (Haswell)	o/f	2,7	P35950 P36144
Haswellia cf. *juxtacarnea*	o/f	2,7	P35951 P36159-60
Ischromene ?polytyla	r/n	7	P35953 P36165-6
Limnoria sp.	r/a	2,7	P35952 P36157-8
?*Paracilicaea* sp.	u/f	2,7	P36622
Paracassidina pectinata Baker	o/f	9	P35963 P36179
Pseudolana towrae Bruce	o/f	5,9	P35966-7
Serolis minuta Beddard	o/f	9	P35964-5
Sphaeromatid sp. 1	o/f	2	P35956

Appendix cont'd.

Sphaeromatid sp. 2	o/f	9	P35962
Sphaeromatid sp. 3	u/f	2,7	P36620
Sphaeromatid sp. 4	o/f	2	P36621
Sphaeromatid sp. 5	o/f	7	P36630
Syncassidina aesturia Baker	u/f	3,4,5	P35968 P36143
SUBORDER: ONISCOIDEA			
Oniscoidean sp. 1	o/f	4,5	P36633-6
Oniscoidean sp. 2	o/f	6	P36632
SUBORDER: VALVIFERA			
Euidotea cf. *peronii*	o/f	9	P36068
Microarcturus sp.	o/f	9	P36071
Neoarcturus sp.	o/f	9	P36070
Pseudarcturella sp.	o/f	9	P36072
Synidotea sp.	o/f	9	P36069
SUBORDER: ASELLOTA			
Ianiropsis sp.	r/n	2,7	P35658-9 P36152-3
Iathrippa sp.	r/n	2,7	P35653-5 P36150-1
Jaeropsis sp. 1	r/n	2,7	P35660-2 P36163-4
Jaeropsis sp. 2	o/f	2	P36064-5
Janirid sp. 1	o/f	7	P36066
Janirid sp. 2	o/f	7	P36067
Stenetrium armatum Haswell	u/n	7	P35650-2 P36161-2
Stenetrium cf. *armatum*	o/f	2	P36063
ORDER: AMPHIPODA			
SUBORDER: GAMMARIDEA			
FAMILY: AMPELISCIDAE			
Ampelisca dimboola Lowry & Poore	o/f	9	P36660
Ampelisca euroa Lowry & Poore	r/f	2,3,7	P36638
Byblis bega Lowry & Poore	o/f	9	P36659
FAMILY: AMPHILOCHIDAE			
Cyproidea ornata Haswell	r/n	2,3	P36709
Narapheonoides mullaya J. L. Barnard	o/f	3	P36708
FAMILY: AMPITHOIDAE			
Ampithoe sp. 1	o/a	2	P36005
Ampithoe sp. 2	u/f	2,3,7	P36712
Ampithoe sp. 3	u/f	7	P36706
Ampithoe sp. 4	o/f	2	P36713
Ampithoe sp. 5	o/f	7	P36707
Cymadusa sp. 1	u/f	7	P35993
Cymadusa sp. 2	o/f	3	P36710
?*Pseudopleonexes* sp.	o/f	7	P36705
FAMILY: ANAMIXIDAE			
Anamixis sp.	o/f	2	P36651 P36714
FAMILY: AORIDAE			
Aora hebes Myers & Moore	r/n	7	P35992 P36187-8
Aora maculata (Thomson)	u/n	2,7	P36014-5
Aora mortoni (Haswell)	r/n	2,3,9	P36032 P36181
Lemboides australis (Haswell)	r/a	2,3,7	P36031 P36189

Appendix cont'd.

Lembos aequimanus Schellenberg	r/f	2,3	P36033 P36180
Xenocheira fasciata Haswell	o/f	2	P36007
FAMILY: COROPHIIDAE			
Corophium sp.	r/n	2,3,7	P36641
Paracorophium ?excavatum	r/n	4,5,6	P36042
Siphonoecetes spp.	o/f	7,9	P36295-306
FAMILY DEXAMINIDAE			
Atylus homochir Haswell	r/a	2,3	P36029
Haustoriopsis sp. 1	r/a	3	P36028
Haustoriopsis sp. 2	o/f	3	P36027
Paradexamine churinga J. L. Barnard	o/f	2	P36005
Paradexamine dandaloo J. L. Barnard	o/f	9	P36043
Paradexamine frinsdorfi Sheard	u/f	7	P35991
Paradexamine lanacoura J. L. Barnard	r/a	2,3	P36026
Paradexamine ?quarallia	o/f	3	P36711
Paradexamine ?thadalee	r/n	2,3,7	P36025 P36203
Polycheira tenuipes Haswell	o/f	7	P36703
Syndexamine cf. *runde*	o/f	2	P36009
Syndexamine sp. 1	u/f	3	P36024
FAMILY: EUSIRIDAE			
Gondogeneia microdeuteropa (Haswell)	r/a	2,7	P35973
Meteusiroides sp.	r/a	2,7	P36004
?*Paramoera* sp.	o/f	2,7	P36012
Tethygeneia nalgo J. L. Barnard	r/n	2,3,7	P36010
Tethygeneia waminda J. L. Barnard	o/n	7,9	P36040
FAMILY: EXOEDICEROTIDAE			
Exoediceroides maculosus (Sheard)	o/f	4	P35639
FAMILY: HYALIDAE			
Hyale crassicornis (Haswell)	r/f	2,7	P35977 P36185-6
Hyale cf. *loorea*	u/a	7	P36645
Hyale maroubrae Stebbing	u/f	2,7	P36013 P36184
Hyale rubra (Thomson)	u/f	2,7	P36182-3 P35976
Hyale sp.	r/f	2,7	P36646
FAMILY: ISAEIDAE			
Ampelisciphotis sp.	r/n	2,3,7,9	P36030
Cheiriphotis sp.	o/f	2,7,9	P35994-5
Gammaropsis sp.	r/a	2,3,7	P36003
?*Gammaropsis* sp. 1	r/n	2,7	P35985
?*Gammaropsis* sp. 2	u/f	2,7	P36002
?*Gammaropsis* sp. 3	r/a	2,7	P35984
Photis sp. 1	r/n	2,3,7,9	P36034-5 P36190-1
Photis sp. 2	o/f	9	P36018 P36102-4
FAMILY: ISCHYROCERIIDAE			
Cerapus sp.	o/f	3,9	P36195-202 P36006
Ericthonius sp.	r/n	2,3,7	P36023
Parajassa sp.	u/n	3,7	P36704
FAMILY: LEUCOTHOIDAE			
Leucothoe assimilis J. L. Barnard	o/f	7	P36642

Appendix cont'd.

Leucothoe boolpooli J. L. Barnard	r/n	2,3,7	P35990 P36213
Leucothoe commensalis Haswell	r/a	2,3,7	P35983 P36214
Paraleucothoe novaehollandiae (Haswell)	r/a	2,7	P35989 P36215
FAMILY: LILJEBORGIIDAE			
Liljeborgia aequabilis Stebbing	r/a	2,3,7	P36001 P36216
Liljeborgia sp. 1	o/f	3	P36022
Liljeborgia sp. 2	o/f	9	P36038
FAMILY: LYSIANASSIDAE			
Amaryllis sp. 1	o/f	2,7	P36700
Amaryllis sp. 2	o/f	2,3,9	P36701
Amaryllis sp. 3	r/a	2,7	P35982 P36702
Lysianassid sp. 1	u/f	7	P35981 P36212
Parawaldeckia dilkera J. L. Barnard	r/f	2,3,7	P36021 P36211
Parawaldeckia sp.	r/f	9	P36207-9 P36044-5
Tryphosella camelus (Stebbing)	u/f	2,3,9	P36016-7 P36210
Uristidid sp. 1	o/f	9	P36204-6 P36036
Waldeckia sp.	r/n	7	P35988
FAMILY: MELITIDAE			
Ceradocus ramsayi (Haswell)	r/n	2,7	P35987 P36229
Ceradocus rubromaculatus (Stimpson)	r/f	2,3,7	P36637
Ceradocus serratus (Bate)	u/f	2,3	P36000 P36218-9
Ceradocus sp.	o/f	2	P36650
?*Ceradocus* sp.	r/f	2,3,7	P36644
Dulichiella australis (Haswell)	r/n	2,7	P35980 P36221
Elasmopus bollonsi Chilton	u/n	7	P35979 P36230
Elasmopus ?yunde	o/f	7	P36644
Gammarella berringar (J. L. Barnard)	o/f	2	P35999
Gammarella mokari (J. L. Barnard)	u/f	2	P35998 P36224-6
Maera viridis Haswell	r/n	2,7	P35978 P36222-3
Maera sp.	o/f	2	P36649
?*Maera* sp.	r/n	2,7	P36643
Mallacoota subcarinata Haswell	o/f	7	P35988
Melita matilda J. L. Barnard	r/a	1,4,6	P36041 P36227-8
Melita sp.	u/f	2,7	P36647-8
Victoriopisa australiensis (Chilton)	r/a	4,5,6	P36699
FAMILY: PARACALLIOPIIDAE			
Paracalliope sp.	r/n	1,4,6	P35637-8
FAMILY: PHLIANTIDAE			
Gabophlias olono J. L. Barnard	u/f	2	P36011 P36220
Iphiplateia whiteleggei Stebbing	o/f	3	P36020

Appendix cont'd.

FAMILY: PHOXOCEPHALIDAE			
Birubius mayamayi Barnard & Drummond	o/f	2	P36691
Birubius muldarpus Barnard & Drummond	o/f	7	P36698
Birubius cf. *nammuldus*	o/f	2	P36690
Birubius quearus Barnard & Drummond	r/f	2,3	P36694-5
?*Birubius* sp.	o/f	9	P36697
Brolgus tattersalli (J. L. Barnard)	o/f	2	P36692
Tipimegus dinjerrus Barnard & Drummond	o/f	9	P36696
Wildus sp.	r/a	3	P36693
FAMILY: PODOCERIDAE			
Podocerus sp. 1	o/a	2	P35997
Podocerus sp. 2	r/n	2,3,7	P35996 P36232-3
Podocerus sp. 3	r/a	2,3,7	P36019 P36231
FAMILY: SYNOPIIDAE			
Tiron sp.	o/f	9	P36039
FAMILY: TALITRIDAE			
Orchestia ?australis	r/f	1,6	P36037 P36217
Orchestia sp.	u/f	2,7	P35974 P35975
FAMILY: UROHAUSTORIIDAE			
Gheegerus cf. *garbaius*	o/f	9	P36661
Tottungus ?tungus	o/f	5	P36652
Urohaustorius gunni Barnard & Drummond	o/f	9	P36658
Urohaustorius merkanius Barnard & Drummond	o/f	9	P36656
Urohaustorius metungi Fearn-Wannan	u/f	5	P36653-4
Urohaustorius parnggius Barnard & Drummond	o/f	9	P36657
Urohaustorius ?urungari	o/f	9	P36655
SUBORDER: CAPRELLIDEA			
Caprella danilevskii Czerniavski	o/f	2	P36684-5
Caprella equilibra Say	o/f	7	P36688-9
Caprella scaura Templeton			P36676-7
?*Hircella cornigera*	o/f	7	P36687
Orthoprotella cf. *mayeri*	u/f	2,3	P36681-3
Paraproto spinosa (Haswell)	o/a	2	P36686
?*Paraproto* sp.	u/f	3	P36678-90
SUPERORDER: EUCARIDA			
ORDER: DECAPODA			
SUBORDER: NATANTIA			
SECTION: PENAEIDEA			
Penaeus plebejus Hess	u/f	1,3,4,5,6	P36102-3 P36668
?*Penaeus* sp. (juv.)	o/f	3	P36106
SECTION: CARIDEA			
Alpheus euphrosyne richardsoni Yaldwyn	u/f	1,2,5	P36100 P36666
Alpheus socialis Heller	u/f	7	P36115
Alpheus sp.	u/f	3,7	P36664-5
Alope ?orientalis	*o/f*	*7*	*P36663*
Hippolyte caradina Holthius	u/a	3	P36108
Hippolyte ventricosa Milne-Edwards	o/f	7	P36110
Palaemon affinis Milne-Edwards	r/a	1,3,4,5,6	P36101
Palaemon serenus Heller	o/f	2	P36667
Rhynchocinetes ?rugulosus	o/a	7	P36662
Synalpheus tumidomanus (Paulson)	u/f	2,7	P36105

Appendix cont'd.

SUBORDER: REPTANTIA			
SECTION: MACRURA			
SUPERFAMILY: THALASSINIDEA			
Axiopsis australiensis De Man	o/f	2	P36104
Callianassa arenosa Poore	u/f	5	P36099
SECTION: ANOMURA			
Diogenes custos affinis Henderson	o/f	9	P36111
Diogenes senex Heller	o/f	3,5	P36098
Paguristes squamosus McCulloch	o/f	3,7	P36107
Pagurus ?lacertosus nana	o/f	7	P36109
Pagurus sinuatus (Stimpson)	o/f	7	P36669
Pagurus sp.	o/f	7	P36670
SECTION: BRACHYURA			
Actaea peronii (Milne-Edwards)	o/f	7	P36083
Amarinus paralacustris (Lucas)	u/f	1	P36090
Carcinus maenas (Linnaeus)	r/a	1,2,6	P36248-9 P36089
Cyclograpsus audouinii Milne-Edwards	r/n	2,6,7	P36076 P36239
Cyclograpsus cf. *audouinii*	o/f	7	P36080
Halicarcinus ovatus Stimpson	r/n	2,3,7,9	P36095 P36234-6
Heloecius cordiformis Milne-Edwards	o/f	5	P36086 P36247
Helograpsus haswellianus (Whitelegge)	r/n	1,6	P36091 P36242-3
Hymenosoma hodgkini Lucas	o/f	5	P36087
Leptograpsus variegatus (Fabricius)	r/a	2,7	P36079
Macrophthalmus latifrons Haswell	u/a	5	P36085 P36245-6
Mictyris longicarpus Latreille	r/n	5,6	P36084
Naxia deflexifrons Haswell	o/f	7	P36673
Notomithrax minor (Filhol)	u/a	3,7	P36094
Notomithrax ursus (Herbst)	o/f	3,7	P36675
Ovalipes australiensis Stephenson & Rees	o/f	1,6	P36088 P36126
Ovalipes sp. (juv.)	o/f	9	P36097
Ozius truncatus (Milne-Edwards)	r/a	2,7	P36081 P36238
Pachygrapsus laevimanus Stimpson	u/a	2,7	P36075
Paragrapsus laevis (Dana)	r/n	1,6	P36092 P36240-1
Petalomera lateralis (Gray)	o/f	2	P36073
Pilumnus rufopunctatus Stimpson	r/a	2,7	P36082 P36237
Pilumnus serratifrons (Kinahan)	r/f	1,2,5,6	P36077
Pilumnus sp.	o/f	7	P36671
Pinnotheres hickmani (Guiler)	o/f	7	P36672
Plagusia chabrus (Linnaeus)	r/f	2,7	P36074
Plagusia glabra Dana	u/f	7	P36078
Portunus pelagicus (Linnaeus)	o/f	3,9	P36096
Sesarma erythrodactyla Hess	r/f	2,5,6	P36244
Xanthias elegans (Stimpson)	o/f	2	P36674
?Xanthid (juv.)	o/f	1,6	
Decapod Larvae	o/f	7,9	
CLASS: PYCNOGONIDA			
Pycnogonid spp.	u/f	2,7	P36549-61

Appendix cont'd.

PHYLUM: SIPUNCULIDA			
Sipunculan spp.	r/a	2,3,5,7	W201423
PHYLUM: BRACHIOPODA			
Magellania flavescens (Lamarck)	o/f	2	C150562
PHYLUM: ECHINODERMATA			
CLASS: ASTEROIDEA			
ORDER: VALVATIDA			
FAMILY: ASTERINIDAE			
Patiriella calcar (Lamarck)	u/a	7	J19849-52 J19887
Patiriella exigua (Lamarck)	r/n	2,7	J19865-73 J19875-76 J198788-92
Patiriella gunni (Gray)	u/a	7	J19853-54 J19874
FAMILY: OREASTERIDAE			
Nectria ocellata E. Perrier	o/f	7	J19855
FAMILY: ASTEROPSEIDAE			
Petricia vernicina (Lamarck)	u/a	2,7	J19856-8
ORDER: SPINULOSIDA			
FAMILY: ECHINASTERIDAE			
Plectaster decanus (Müller & Troschel)	o/f	7	J19864
ORDER: FORCIPULATIDA			
FAMILY: ASTERIIDAE			
Coscinasterias calamaria (Gray)	r/n	2,3,7	J19884-5 J19834-48
Uniophora granifera (Lamarck)	o/a	7	J19859-63
CLASS: OPHIUROIDEA			
ORDER: OPHIURIDAE			
FAMILY: OPHIOCOMIDAE			
Clarkcoma pulchra (H. L. Clark)	o/f	2	J19832
FAMILY: OPHIONEREIDAE			
Ophionereis schayeri (Müller & Troschel)	u/n	2,7	J19826-9
FAMILY: OPHIACANTHIDAE			
?*Ophiacantha* sp.	o/f	9	J19895
FAMILY: OPHIACTIDAE			
Ophiactis resiliens Lyman	o/a	7	J19902-5 J10008-9 J20002
FAMILY: AMPHIRORIDAE			
Amphipholis squamata (Delle Chiaje)	of	2,3,9	J20001 J19899-901
Amphiura constricta Lyman	u/f	2,3,7	J19881-3 J19906
Amphiura micra H. L.Clark	o/f	2,3,7,9	J19877-79 J19907
FAMILY: OPHIOTHRICIDAE.			
Ophiothrix (Ophiothrix) caespitosa Lyman	o/f	7	J19893-4
Ophiothrix (Ophiothrix) cilaris (Lamarck)	o/f	7	J19995-7
Ophiothrix (Placophiothrix) spongicola Stimpson	o/f	7	J19831
CLASS: ECHINOIDEA			
ORDER: CIDAROIDA			
FAMILY: CIDARIDAE			
Phyllacanthus parvispinus Tenison-Woods	r/f	7	J19823-5

Appendix cont'd.

ORDER: DIADEMATOIDA			
FAMILY: DIADEMATIDAE			
Centrostephanus rodgersii (A. Agassiz)	r/a	2,7	J19815
ORDER: TEMNOPLEUROIDA			
FAMILY: TEMNOPLEURIDAE			
Holopneustes inflatus A. Agassiz	o/f	2,7,9	J19910
ORDER: ECHINOIDA			
FAMILY: ECHINOMETRIDAE			
Heliocidaris erythrogramma (Valenciennes)	r/a	2,3,7	J19816-21
Heliocidaris tuberculata (Lamarck)		2,7	J19822
CLASS: HOLOTHUROIDEA			
ORDER: DENDROCHIROTIDA			
FAMILY: CUCUMARIIDAE			
Pentacta ignava (Ludwig)	o/f	2,7	J19896-8
Pseudocnus sp.	u/a	2	J19909
ORDER: MOLPAPIIDA			
FAMILY: CAUDINIDAE			
Paracaudina chilensis var. *ransonnetti* (von Marenzeller)	o/f	9	J19908
CLASS: CRINOIDEA			
ORDER: COMATULIDA			
FAMILY: COMASTERIDAE			
Cenolia tasmaniae (A. H. Clark)	o/f	7	J19833
PHYLUM: CHORDATA			
SUBPHYLUM: TUNICATA			
CLASS: ASCIDIACEA			
ORDER: PLEUROGONA			
FAMILY: STYELIDAE			
Styela plicata (Lesueur)	o/f	3	Y2060
FAMILY: PYURIDAE			
Herdmania momus (Savigny)	r/n	2,7	Y2061-65
Pyura gibbosa (Heller)	r/n	2,7	Y2057-59
Pyura spinifera (Quoy & Gaimard)	o/f	7	Y2049
Pyura stolonifera (Heller)	r/n	7	Y2050-56
PHYLUM: CHORDATA			
GRADE: PISCES			
ORDER: AMPHIOXIFORMES			
FAMILY: BRANCHIOSTOMATIDAE			
Amphioxus sp.	o/f	9	I26021-002
ORDER: ANGUILLIFORMES			
FAMILY: ANGUILLIDAE			
Anguilla australis Richardson	o/f	4,6	I26017-001 I26018-001
FAMILY: OPHICHTHIDAE			
Muraenichthys sp.	o/f	9	I26019-001
ORDER: SCORPAENIFORMES			
FAMILY: SCORPAENIDAE			
Ruboralga ergastulorum (Richardson)	o/f	3	I26007-001
Scorpaenidae sp.	o/f	4,6	I26015-003
Centropogon australis (White)	o/f	6	I26015-002
ORDER: PERCIFORMES			
FAMILY: CLINIDAE			
Heteroclinus heptaeolus (Ogilby)	o/f	2,7	I26008-001 I26010-001

Appendix cont'd.

FAMILY: GOBIIDAE			
Arenigobius bifrenatus (Kner)	o/f	5	I26020-001
Favonigobius tamarensis (Johnson)	o/f	5	I26014-002
Philypnodon grandiceps (Kreft)	o/f		I26016-001
Pseudogobius olorum (Sauvage)	o/f	1,5,6	I26013-001 I26014-001 I26015-001
Pseudogobius sp.	o/f	1	I26011-001 I26009-001
FAMILY: SERRANIDAE			
Epinephelus sp.	o/f	7	I26012-001

The Dictyotales (Algae: Phaeophyta) of New South Wales

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FARRANT, P. A., KING, R. J. The Dictyotales (Algae: Phaeophyta) of New South Wales. *Proc. Linn. Soc. N.S.W.* 110(4), (1988) 1989: 369-405.

A survey is given of the Dictyotales (Phaeophyta) on the New South Wales mainland coast. Twenty-two species are recognized in 13 genera: *Dictyopteris*, *Dictyota*, *Dilophus*, *Distromium*, *Homoeostrichus*, *Lobophora*, *Lobospira*, *Pachydictyon*, *Padina*, *Spatoglossum*, *Stypopodium*, *Taonia*, and *Zonaria*. For each, a concise description with illustrations, based on New South Wales material, is presented. Keys are provided to genera and species.

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INTRODUCTION

Brown algae in the Order Dictyotales Kjellman are a conspicuous component of the lower eulittoral and sublittoral marine flora of the New South Wales coast (King and Farrant, 1987). Many specimens, especially immature plants, of the Dictyotales on the New South Wales coast have been difficult to identify despite publications from southern Queensland (Cribb, 1954), southern Australia (Womersley, 1967, 1987) and Lord Howe Island, New South Wales (31°33′S, 159°05′E) (Allender and Kraft, 1983). Lord Howe Island is administratively part of New South Wales, but it is as far removed from the mainland New South Wales coast as are much of Queensland and Victoria (Fig. 1).

The Dictyotales is a distinctive order and members can be recognized by a flattened thallus with apical growth, tufts of surface hairs and oogamous reproduction with characteristic antheridia and oogonia on or embedded in the thallus surface (Womersley, 1987). The plants are usually erect or occasionally decumbent in habit. The fronds are either dichotomous, subdichotomous or irregular if growth is initiated by a single apical cell or a small group of apical cells, or flabellate or irregular if growth is from a row of marginal cells.

The Dictyotales have been placed traditionally in a single family, the Dictyotaceae, within which two tribes were recognized: the Dictyoteae, characterized by a single apical cell, and the Zonarieae with a group or marginal row of apical cells. Womersley (1987) notes that two families, the Dictyotaceae and the Zonariaceae, may seem warranted, but that their recognition is not satisfactory for some juvenile stages. There are two genera which, though clearly members of the Dictyotales, are sufficiently distinct to warrant placement in separate families. Allender (1980) placed the genus *Dictyotopsis* Troll in a new family, Dictyotopsidaceae. In this family the single apical cell segments laterally and the thallus is monostromatic. In those members of the Dictyotaceae which possess a single apical cell it is oriented transversely to the branch apex or is conical and new cells are cut off only from the lower side (Womersley, 1987). *Dictyotopsis*, represented by the single species *D. propagulifera* Troll, has not been found on New South Wales shores though sterile plants have been recorded by one of us (R.J.K.) associated with mangroves in Queensland (near the mouth of the Endeavour River and at Hinchinbrook Island). Womersley (1987) has described a new family, the Scoresbyellaceae, for the distinctive monotypic genus *Scoresbyella*. The plants resemble those in the Dictyoteae, but

Fig. 1. Locality map.

the apical cell is oriented longitudinally and cells are cut off laterally from two faces rather than from one basal side. *Scoresbyella profunda* Womersley appears to be a rare alga and is thus far known from only a few deep-water collections in South Australia.

The total number of genera in the order Dictyotales is 18 and there are approximately 100 species. All genera except *Stoechospermum* have been recorded in Australia. Fifteen genera and 41 species occur on temperate southern Australian coasts (Womersley, 1987). This contrasts with the generalization that the order is best developed on tropical and subtropical coasts (Haupt, 1932; Bold and Wynne, 1985). Table 1 shows the number of genera and species in various regions of Australia and indicates that the order Dictyotales is well represented in both northern and southern Australia. The high figure for southern Australia reflects the richness of the well-documented algal flora (Womersley, 1981, 1987). The comparable figure for northern Australia is based upon species records only (not including those for Lord Howe Island) (Lewis, 1985), and may be artificially high, especially for *Dictyota*. Of the 44 species recorded in northern Australia, approximately 24 are recorded for Queensland and Norfolk Island, a number similar to that for southern Queensland (20), New South Wales (22), and Lord Howe Island (22).

MATERIALS AND METHODS

Members of the Order Dictyotales were collected on a regular basis at Fairlight in Sydney Harbour (33°50′S, 151°15′E) in an associated study of the phenology of

TABLE 1

Number of species in the Order Dictyotales recorded for various regions of Australia: northern Australia (after Lewis, 1985), southern Queensland (after Lewis, 1985: Cribb, 1954; N.S.W. herbarium specimens), Lord Howe Island (Allender and Kraft, 1983), New South Wales (this study) and southern Australia (Womersley, 1987)

	nthn Aust.	**sthn Qld**	**Lord Howe Island**	**N.S.W.**	**sthn Aust.**
ORDER DICTYOTALES					
F. DICTYOTACEAE					
Dictyoteae					
Dictyota	15	6	3	3	7
Dilophus	3	2	2	2	7
Glossophora	2	0	0	0	1
Pachydictyon	0	0	1	1	2
Zonarieae					
Chlanidophora	0	0	0	0	1
Dictyopteris	7	3	5	1	5
Distromium	0	0	1	1	2
Homoeostrichus	0	0	0	2	3
Lobophora	1	1	1	1	1
Lobospira	0	0	0	1	1
Padina	6	6	4	4	4
Spatoglossum	3	1	1	1	1
Stypopodium	3	0	2	1	0
Taonia	1	0	1	1	1
Zonaria	2	1	1	3	4
F. DICTYOTOPSIDACEAE					
Dictyotopsis	1	0	0	0	0
F. SCORESBYELLACEAE					
Scoresbyella	0	0	0	0	1
Total Genera: 17 Species:	44	20	22	22	41

members of the order (King and Farrant, 1987). In addition, collections were made at other localities in New South Wales, but the majority of collections made were from the Sydney region. Localities in the Sydney metropolitan area include Camp Cove, Dobroyd, Fairlight, Lady Jane Beach, Mrs Macquarie's Point, Point Piper and Vaucluse in Sydney Harbour; Bare Island in Botany Bay; Church Point in Pittwater; and Boat Harbour, Clovelly, Collaroy, Fairy Bower, Harbord, Long Bay, Long Reef and Newport on the nearby open coast. Localities in the Jervis Bay area include Plantation Point (inside the bay), Crookhaven Heads (north of the bay) and Steamers Beach (south of the bay). All New South Wales localities other than these can be found in the Reader's Digest Atlas of Australia (1977) or in Fig. 1. Voucher specimens (herbarium sheets and wet material) are lodged in the John T. Waterhouse Herbarium, University of New South Wales (UNSW). Herbarium material from NSW (including the A. H. S. Lucas collection), UNSW, MELU, and selected specimens from MEL and MUCV were examined during the course of the study.

RESULTS

The order Dictyotales in New South Wales is represented by 22 species in 13 genera (Table 2). A key to the genera is presented below and this is followed by a description of each species **based on mature specimens from the New South Wales coast**. Where a genus is represented by more than one species, a key to the species is given. The descriptions are concise and do not repeat detailed information and complete lists of synonymy readily available elsewhere (especially in Allender and Kraft, 1983; and Womersley, 1987). Rather they concentrate on information necessary for the identification of the taxa. Only where a species has been widely referred to by another name is the synonym given. Seasonality, seasonal and spatial variation in abundance, and seasonal variation in fertility for some of the common species are given by King and Farrant (1987).

TABLE 2

Species of Dictyotales in New South Wales

Dictyopteris acrostichoides (J. Agardh) Boergesen
Dictyota alternifida J. Agardh
Dictyota bartayresii Lamouroux
Dictyota dichotoma (Hudson) Lamouroux
Dilophus intermedius (Zanardini) Allender and Kraft
Dilophus marginatus J. Agardh
Distromium flabellatum Womersley
Homoeostrichus olsenii Womersley
Homoeostrichus sinclairii (Hooker and Harvey) J. Agardh
Lobophora variegata (Lamouroux) Womersley
Lobospira bicuspidata Areschoug
Pachydictyon paniculatum (J. Agardh) J. Agardh
Padina australis Hauck
Padina crassa Yamada
Padina fraseri (Greville) Greville
Padina tenuis Bory
Spatoglossum macrodontum J. Agardh
Stypopodium flabelliforme Weber-van Bosse
Taonia australasica J. Agardh
Zonaria angustata (Kuetzing) Papenfuss
Zonaria crenata J. Agardh
Zonaria diesingiana J. Agardh

The most abundant species, in terms of cover and biomass, in the Sydney area is *Zonaria diesingiana*. Some species are apparently rare (*Padina australis*) or rare but nonetheless widely distributed in New South Wales (*Zonaria crenata*). Other species have more restricted distributions in southern New South Wales (*Lobospira bicuspidata*, *Pachydictyon paniculatum*, *Zonaria angustata*) though they are otherwise more widely distributed in southern Australia. Some collections made in the course of this study were new records, e.g. *Homoeostrichus olsenii* (reported in Womersley, 1987) and *Distromium flabellatum*. Three genera are present in southern Australia but absent from New South Wales: *Scoresbyella*, *Chlanidophora* and *Glossophora*. The record of *Glossophora nigricans* from Plantation Point, New South Wales (May and Larkum, 1981) is of *Dilophus intermedius*. Only one genus, *Stypopodium*, is present in New South Wales but absent on the southern Australian coast. Only two genera (*Homoeostrichus* and *Lobospira*), occur on the New South Wales mainland coast but not at Lord Howe Island, but all the genera at Lord Howe Island are found on the mainland coast.

KEY TO THE DICTYOTALES IN NEW SOUTH WALES

1. Growth initiated by a single apical cell 2
1.* Growth initiated from a marginal row or cluster of apical cells 4
2. Thallus with a single cortical layer and a single medullary layer throughout . . . . *Dictyota*

2.* Thallus with more than one layer of either cortical cells or medullary cells, at least along margins 3
3. Medulla single-layered, cortex two or more cells thick in older thallus parts, at least at the margins .... *Pachydictyon*
3.* Medulla two or more cells thick, at least at the margins, cortex single-layered throughout .... *Dilophus*
4. Meristem a localized cluster of apical cells 5
4.* Meristem of terminal row of apical cells 7
5. Thallus with thickened terete axis and slender flat branches with ultimate divisions spirally twisted and bicuspidate .... *Lobospira*
5.* Thallus flattened throughout 6
6. Frond with a prominent midrib .... *Dictyopteris*
6.* Frond without a prominent midrib .... *Spatoglossum*
7. Apical margin of the thallus inrolled .... *Padina*
7.* Apical margin of the thallus not inrolled 8
8. Thallus two cells thick throughout .... *Distromium*
8.* Thallus more than two cells thick, at least in mature parts 9
9. Medullary cells rectangular and in regular tiers in transverse section 10
9.* Medullary cells neither uniformly rectangular nor in regular tiers in transverse section 12
10. Central medullary cells distinctly larger than other medullary cells in transverse section .... *Lobophora*
10.* Medullary cells of similar size throughout transverse section 11
11. Generally paired cortical cells to each medullary cell, sporangia producing eight aplanospores .... *Zonaria*
11.* Generally single cortical cell to each medullary cell, sporangia producing four aplanospores .... *Homoeostrichus*
12. Pronounced size differentiation between smaller pigmented cortical cells and larger colourless medullary cells, distal fronds thick, becoming 4 cells thick several cells below the apex .... *Stypopodium*
12.* No pronounced difference in size between pigmented cortical cells and colourless medullary cells, distal fronds thin, remaining 2 cells thick for some distance below the apex .... *Taonia*

Dictyota Lamouroux

Growth initiated by a single relatively large apical cell. **Thalli** complanate, membranous; fronds with dichotomous or partly pseudo-alternate branching; hair tufts not associated with reproductive organs; in section a single layer of large medullary cells and a single layered cortex of small pigmented cells.

There are three species of *Dictyota* on the New South Wales coast, *D. alternifida*, *D. bartayresii* and *D. dichotoma*.

KEY TO THE SPECIES OF *DICTYOTA* IN NEW SOUTH WALES

1. Fronds broad at the apices, tapering towards the base .... *D. bartayresii*
1.* Fronds linear, or tapering slightly towards the apex 2
2. Fronds narrow, generally about 1 mm wide (range 0.5-4mm [2-4mm wide forms have 2-4cm long internodes and the thallus tends to spiral]) .... *D. alternifida*
2.* Fronds broad, generally greater than 4 mm wide (range 2-14mm [2-4mm forms have internodes shorter than 2cm and the thallus does not tend to spiral]) .... *D. dichotoma*

Dictyota alternifida J. Agardh, 1894:80. Womersley, 1987: 198.

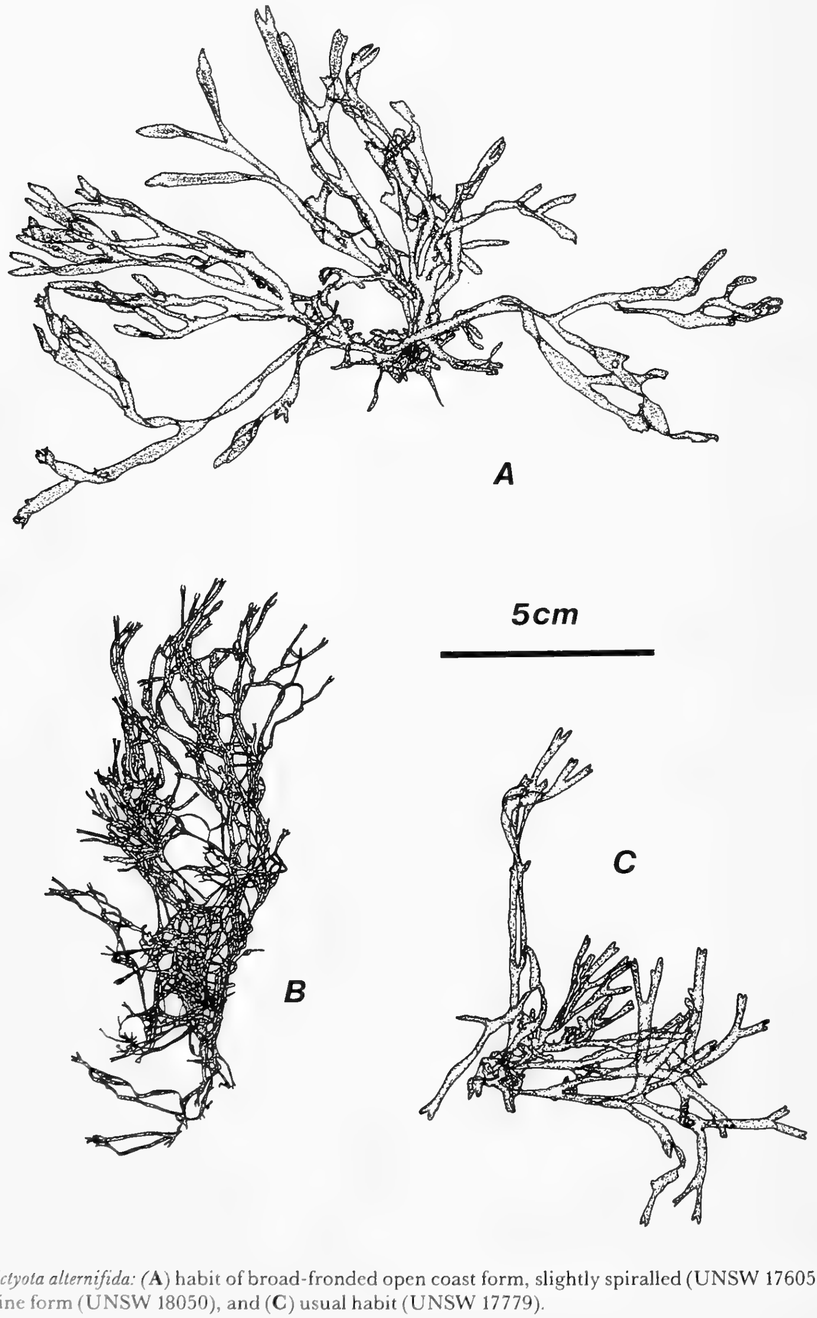


Fig. 2. Dictyota alternifida: (**A**) habit of broad-fronded open coast form, slightly spiralled (UNSW 17605a), (**B**), habit of fine form (UNSW 18050), and (**C**) usual habit (UNSW 17779).

Thalli (5-)7-10(-14)cm long; fronds 0.5-2(-4)mm wide (Fig. 2**A-C**), linear, sometimes twisted, tapering slightly toward the tip, apices usually acute, margins smooth to undulate (occasionally with proliferations); branching dichotomous at 0.5-1.5(-4)cm intervals, with a narrow branching angle (less than 90°, usually 45° or less); sporangia scattered (Fig. 2**A**).

Plants from rough-water localities have wider fronds (to 4mm), but are distinguished from *Dictyota dichotoma* by their longer internodes (2-4cm) and the tendency of the thallus to spiral (Fig. 2**A**). Such plants form a continuous series with more typical *D. alternifida* specimens and can be readily distinguished from *D. dichotoma* in the field. The wide variation in this species and the relationship to other 'narrow' species requires detailed study. Plants referred to *D. alternifida* from New South Wales coastal saline lagoons display unusual thallus variations including frond proliferations, distal crowding of branches, recurved branching angles, apiculate branch ends and spiralling. One unusual specimen from the Coffs Harbour region (UNSW 18605) is here referred to *D. alternifida*, although this may prove to be a different species should more specimens become available.

Seasonality: collected in all months; sporangial plants in all months except January; no sexual material found.

Australian distribution: not previously recorded for New South Wales, although Lucas (1909) recorded the species for northern and southern Australia; the most common species of *Dictyota* in southern Australia (Womersley, 1987); found right along the New South Wales coast in a range of habitats, from shallow sandy sublittoral areas on rough water coasts to positions of extreme shelter in coastal saline lagoons.

Selected specimens examined: New South Wales: Hastings Point, 19-v-1986, *Phillips*, MUCV 2562; Coffs Harbour, 2-4m, 4-x-1981, *Farrant*, UNSW 18050; Hat Head, LWM, 9-x-1985, *P. and W. Farrant*, UNSW 18643; Smiths Lake, 23-iv-1984, *King*, UNSW 16204; Long Reef, 10-vii-1975, *Harada* R2101, NSW; Fairy Bower, 2-3m, 1-xii-1985, *Farrant*, UNSW 18594; Dobroyd, 10m, 24-ix-1985, *Farrant*, UNSW 18530; Clovelly, 1-3m, 28-ii-1985, *Farrant*, UNSW 17659. South Australia: Cape Northumberland (38°03′S, 140°40′E), 15-x-1985, *Womersley*, NSW ex ADU A56812.

Womersley (1987) has noted that species concepts in the genus *Dictyota* are not well established and that the degree of variation in many species is considerable. *Dictyota linearis* J. Agardh and *D. dichotoma* var. *intricata* [both recorded for New South Wales by May (1939)] are here placed under *D. alternifida*. *Dictyota linearis* is characterized by narrow twisted fronds. The majority of the plants from New South Wales do not show this feature, although many fit the description of the species given by Earle (1969) (who nonetheless questions the validity of this species). *Dictyota furcellata* (C. Agardh) J. Agardh was recorded by May *et al.* (1978) and by Borowitzka *et al.* (1982) for New South Wales. All specimens on which these records were based are considered to be *D. alternifida*. We have also placed under *D. alternifida* all narrow forms, including those from coastal saline lagoons.

Dictyota bartayresii Lamouroux, 1809:331. Cribb, 1954:20; Allender and Kraft, 1983:112.

Thalli 5-10cm long; fronds 4-5mm wide at the apices, tapering to 2mm or less at the base; branching sub-dichotomous, dichotomies frequently developing unevenly, branching angle usually 70-90° (Fig. 3**A-C**); sporangia with involucral cells.

Dictyota bartayresii plants in New South Wales exhibit broad obtuse apices and narrow bases as noted by Cribb (1954). The species is extremely variable (Cribb, 1954) and Allender and Kraft (1983) placed plants from Lord Howe Island (which taper to the apices as well as the base) into this taxon. The well-developed striations reported by Allender and Kraft (1983) and seen in some Queensland specimens (e.g. UNSW 15354) are not seen in New South Wales plants.

Seasonality: may be seasonal in New South Wales since most plants collected in the period September-November; only one sporangial plant examined (NSW: *V. May* 1045, Collaroy).

Australian distribution: pantropical, including south-eastern Queensland (Cribb, 1954) and Lord Howe Island (Allender and Kraft, 1983); now recorded for New South Wales, on rocks, 5-15m deep.

Selected specimens examined: New South Wales: Broughton I., 15m, 28-iv-1985, *Farrant*, UNSW 18017; Collaroy, drift, 16-xi-1945, *V. May* 1045, NSW; Long Reef, 15m, 16-xi-1985, *Farrant*, UNSW 18575; Fairlight, 2-3m, 16-ix-1985, *Farrant*, UNSW 18511; Dobroyd, 10m, 24-ix-1985, *Farrant*, UNSW 18531; Clovelly, 27-viii-1987, *D. May*, MUCV 2576; Bare I., 10m, 17-x-1985, *Farrant*, UNSW 18564; Plantation Point, 1-x-1974, *Larkum and May*, NSW.

Dictyota dichotoma (Hudson) Lamouroux, 1809:331. Womersley, 1987:194.

Thalli 3-20cm long, often with a blue-green irridescence *in situ*; fronds 5-10 (-14)mm wide, linear, tapering slightly towards broad apices, without proliferations; branching dichotomous, branching angle 15-45° (Fig. 4**A-D**); sporangia (Fig. 4**E**) scattered, often densely, over both frond surfaces but frequently in broad transverse bands (Fig. 4**A**), best seen in plants *in situ*; sexual plants dioecious, oogonia (Fig. 4**B**,**F**) and antheridia (Fig. 4**C**,**G**) in scattered sori; male plants often recognizable from the more or less circular 'patches' surrounded by involucral cells which remain after the antheridia have been released.

Seasonality: fertile plants year-round; sporangial plants in every month except May; gametangial plants in all but May, August and November (King and Farrant, 1987).

Australian distribution: widely distributed (Womersley, 1967), with numerous records for New South Wales (Gepp and Gepp, 1906; Lucas, 1909, 1914; May, 1939; Cribb, 1954; May *et al.*, 1970); present in bays, estuaries and on rough water coasts at depths to 16m, on rock or other substrata, often epiphytic.

Selected specimens examined: New South Wales: NW Solitary I., 10-16m, 6-x-1985, *Farrant*, UNSW 18613; Coffs Harbour, 28-viii-1980, *Millar*, MELU AM 362; Port Macquarie, 0-2m, 10-x-1985, *P. and W. Farrant*, UNSW 18658; Newport, 21-x-1944, *V. May* 422, NSW; Clovelly, 2-3m, 10-iv-1985, *Farrant and Puttock*, UNSW 17760; Botany Bay, Jan. 1905, *Lucas*, NSW 140397; Bare I., 1-2m, 13-iii-1985, *Farrant and Puttock*, UNSW 17692; Kiama, 20-xi-1945, *V. May 1062*, NSW; Crookhaven Heads, 30-iv-1977, *King and Kertesz*, UNSW 15347.

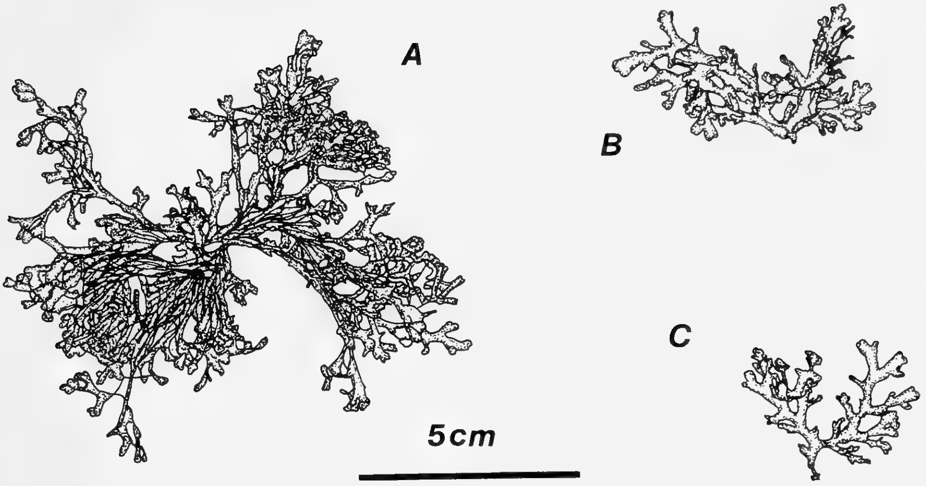
The New South Wales records of *Dictyota papenfussii* Lindauer (Lindauer *et al.*, 1961) and of *D. radicans* Harvey (May, 1939) are here referred to *D. dichotoma*.

Pachydictyon J. Agardh

Growth initiated by a single protruding apical cell. **Thalli** dichotomous, developing axes which bear alternate lateral branch systems; branches compressed (Womersley, 1987); in section consisting of a single-celled medulla, and a multilayered cortex in older, lower axes.

Pachydictyon paniculatum (J. Agardh) J. Agardh 1894:84. Womersley 1987:211.

Thalli 6-10cm long, attached by numerous flattened slender outgrowths from near the base; fronds 0.5-1mm wide in upper parts, lower parts 2-3mm wide; upper branches fastigiate, subdichotomous to lateral (Fig. 5**A**,**B**); hair tufts and sporangia scattered.



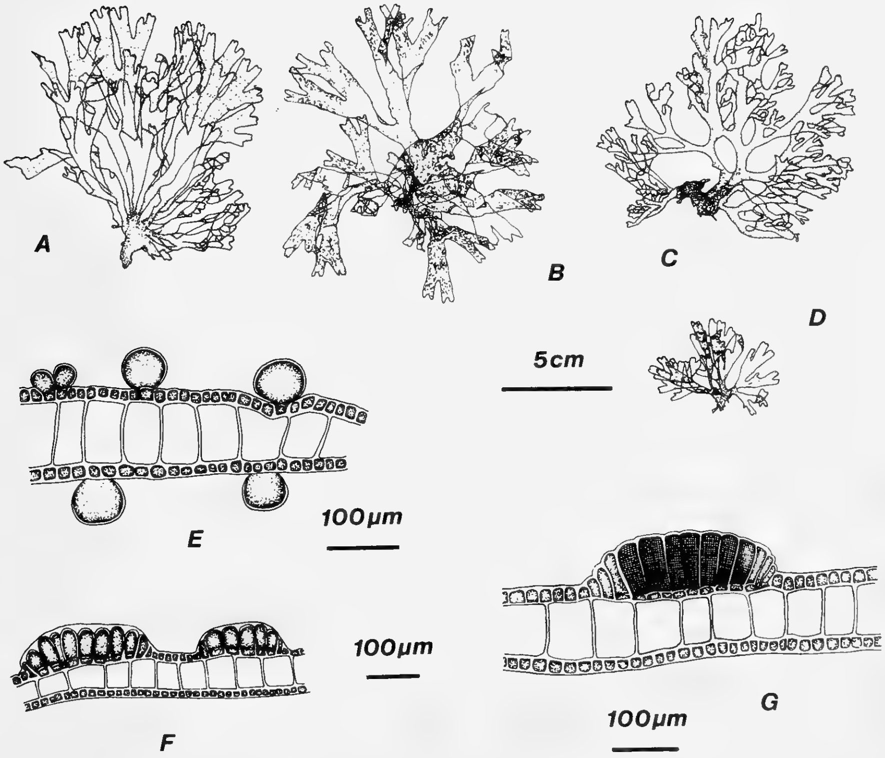


Fig. 3 (above). *Dictyota bartayresii*: (**A**) habit of large plant (UNSW 18554), (**B**) and (**C**) habit of small plants (UNSW 18511).

Fig. 4 (below). *Dictyota dichotoma*: (**A**) habit of sporangial plant (UNSW 18259), (**B**) habit of female plant (UNSW 18069), (**C**) habit of male plant (UNSW 17748), (**D**) small plant (UNSW 17677), (**E**) T.S. sporangial plant (UNSW 18259), (**F**) T.S. female plant (UNSW 18069), and (**G**) T.S. male plant (UNSW 18038, wet material only).

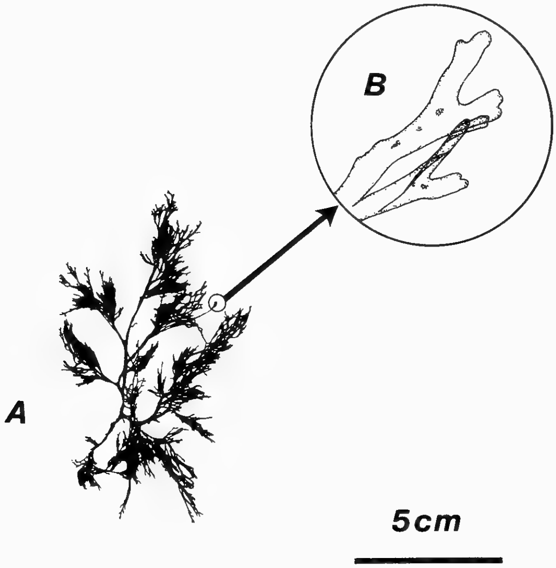


Fig. 5. Pachydictyon paniculatum: (**A**) habit (V. May 2040, NSW), (**B**) frond apex.

New South Wales specimens are smaller than those described from more extensive collections in southern Australia.

Seasonality: early collections made in January (1943, 1946); however no specimens collected in this study.

Australian distribution: in New South Wales appears to be confined to the south coast where it is rare; earlier reports of the species extending as far north as Sydney (e.g. Borowitzka *et al.*, 1982) probably based upon two specimens of *Dictyota* in NSW collected by Lucas and incorrectly identified; in southern Australia epiphytic on larger algae in the upper subtidal under moderate to strong water movement (Womersley, 1987).

Selected specimens examined: New South Wales: Moruya, 7-i-1943, *V. May* 985, NSW; Ulladulla, 13-i-1946, *V. May* 2040, NSW; Green Cape, 1970, *Ducker and King*, MELU 20694. Victoria: Flinders, 5-i-1976, *King*, UNSW 16049.

COMPARISON WITH *PACHYDICTYON* SPECIES IN ADJACENT REGIONS

A second species, *Pachydictyon polycladum* (Kuetzing) Womersley, occurs from Champion Bay, Western Australia to Port Phillip Bay, Victoria (Womersley, 1987), but has not been recorded in New South Wales. A third species of *Pachydictyon* has been recorded for Lord Howe Island. This species, *P. aegerrime* Allender and Kraft, just qualifying as a *Pachydictyon* because on its multicellular cortex, was described on the basis of a single plant, indistinguishable in the field from *Dictyota bartayresii* but lacking horizontal banding, spiralling and involucre cells (Allender and Kraft, 1983).

Dilophus J. Agardh

Growth from a single apical cell. **Thalli** erect, complanate, dichotomously branched or with irregular lateral branching; fronds in section exhibiting a single-celled cortex and a single-celled medulla which becomes multilayered at least at the margins.

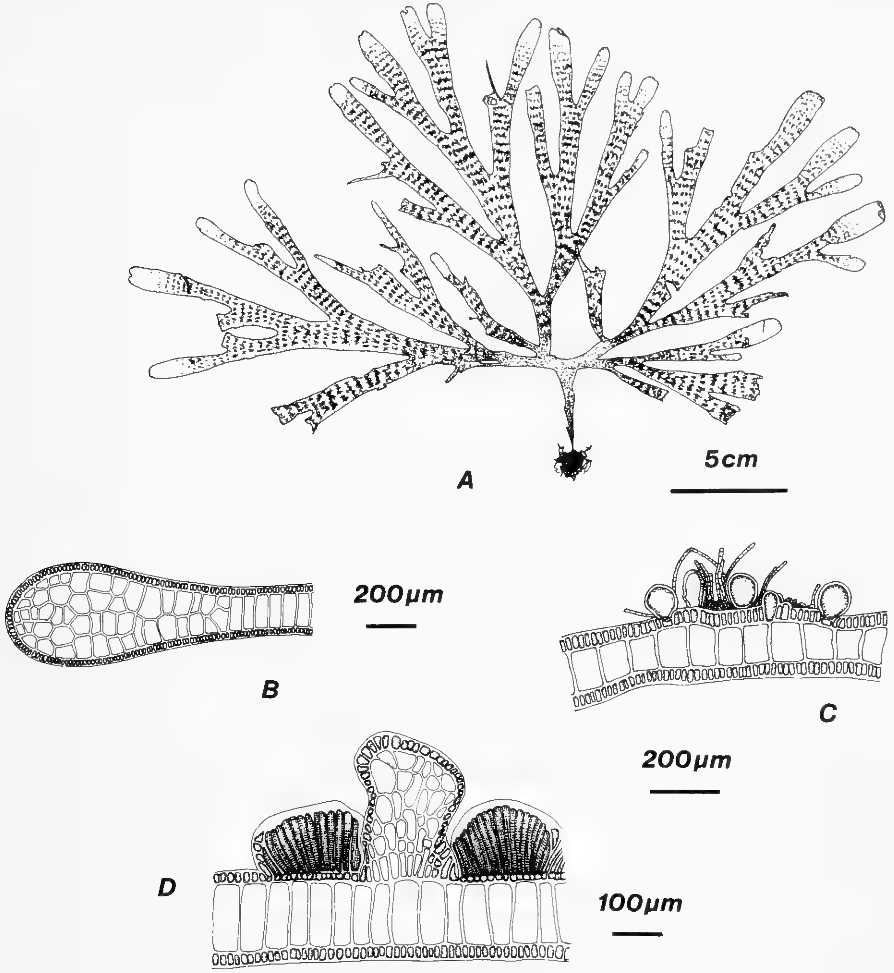


Fig. 6. Dilophus intermedius: (**A**) habit of sporangial plant (UNSW 13789), (**B**) T.S. frond margin (UNSW 18602), (**C**) sporangia (UNSW 17708), (**D**) male gametangia (UNSW 18338).

Two species of *Dilophus* are common on the New South Wales coast: *D. intermedius* and *D. marginatus*.

KEY TO THE SPECIES OF *DILOPHUS* IN NEW SOUTH WALES

1. Mature fronds with branches more than 6mm (usually about 10mm) wide, sori in block-like patches, branches often with abundant flattened proliferations, branches not corrugated . . . . *D. intermedius*

1*. Mature fronds with branches less than 6mm wide, sori scattered, not in block-like patches, branches without proliferations, branches corrugated . . . . *D. marginatus*

Dilophus intermedius (Zanardini) Allender and Kraft, 1983:118.

Thalli 10-40cm long, attached by wiry stolons (Fig. 6**A**); branches 8-13mm (usually about 10mm) wide, often bearing proliferations up to 10mm long in rows across lower frond surfaces; in transverse section medulla 1(-2) cells thick, up to 4-6 cells thick at the margins (Fig. 6**B**); sporangia (Fig. 6**C**) in block-like patterns on the frond surface (Fig. 6**A**); antheridia in indusiate sori (Fig. 6**D**).

The species is apparently very variable (Allender and Kraft, 1983: fig. 25) and we include the collection from Long Reef (MELU GK6921, duplicate in UNSW) within this species. Plants in this collection are dark brown, with diffuse sori rather than block-like sori, and proliferations along the margins which may be consequent on damage.

Seasonality: sporangial plants collected in March, April, May, June and October; male plants found in March and April, the first record of gametangial plants of *Dilophus intermedius*.

Australian distribution: Lord Howe Island, and the mainland coast from Sydney north to Queensland (Allender and Kraft, 1983; Cribb, 1954; Lindauer *et al.* 1961; May, 1939; Gepp and Gepp, 1906); in this survey as far south as Jervis Bay, growing on rocks in the upper sublittoral.

Selected specimens examined: New South Wales: Hastings Point, 19-v-1986, *Phillips*, MUCV 2558; Split Solitary I., 16m, 5-x-1985, *Farrant*, UNSW 18602; Coffs Harbour, 18-iv-1980, *Millar and Mix*, MELU AM 061; Seal Rocks, 0-2m, 10-x-1985, *P. and W. Farrant*, UNSW 18683; Tuggerah Lakes, Apr. 1911, *Lucas*, NSW A1351; Long Reef, 12-vii-1979, *Kraft and Borowitzka*, MELU GK 6921 (duplicate in UNSW: 18400); Fairlight, 1-2m, 20-iii-1986, *Farrant*, UNSW 18338; Fairlight, 1-3m, 14-v-1985, *Farrant*, UNSW 18055; Long Bay, July 1903, *Lucas*, NSW 140425; Jervis Bay, drift, 18-iii-1985, *King*, UNSW 17708. Queensland: Caloundra, Jan. 1909, *Lucas*, NSW 140451.

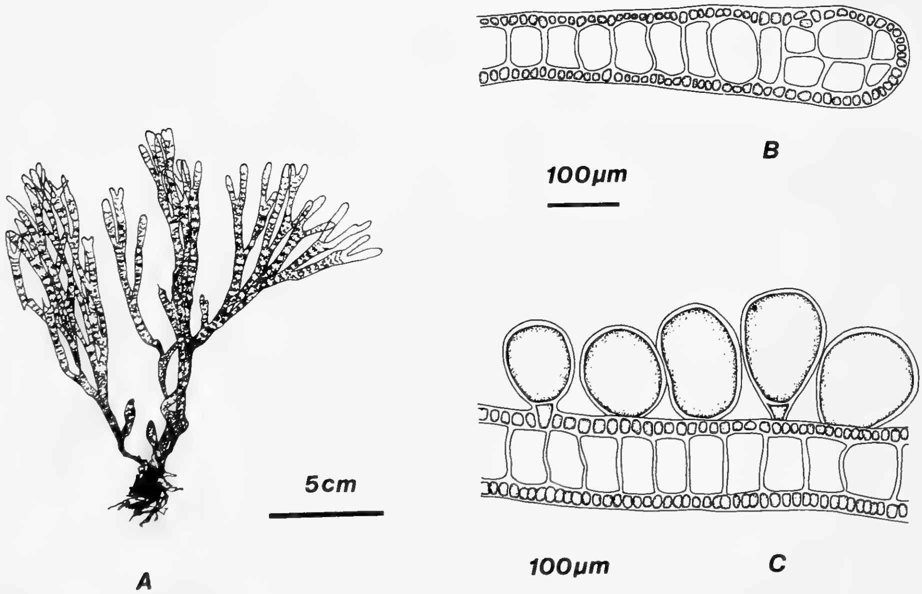


Fig. 7. Dilophus marginatus: (**A**) habit of sporangial plant, with sporangia concealing the wrinkled nature of the thallus (UNSW 18225), (**B**) T.S. frond margin (UNSW 18042), (**C**) sporangia (UNSW 18355).

Dilophus marginatus J. Agardh, 1894:91. Allender and Kraft, 1983:118; Womersley, 1987:202.

Thalli 5-18cm (usually about 10cm) long, basally stoloniferous (Fig. 7**A**); fronds 3-

6mm wide, linear, mature blades corrugated due to transverse wrinkling; hair tufts scattered; in transverse section a single-celled medulla becoming 2(-3) cells thick at the frond margins (Fig. 7**B**); sporangia (Fig. 7**C**) scattered on the frond surface, especially abundant in the corrugations.

Seasonality: present in all months, although abundance was seasonal, peaking in autumn-winter (King and Farrant, 1987); sporangial plants found in all months except December and January; no gametophytic plants known for this species.

Australian distribution: from South Australia to Queensland, and from Lord Howe Island (May, 1939; Cribb, 1954; Allender and Kraft, 1983; Womersley, 1987); common in shallow sublittoral rocky and sandy habitats and lower eulittoral pools.

Selected specimens examined: New South Wales: Hastings Point, 19-v-1986, *Phillips*, MUCV 2557; NW Solitary I., 10-16m, 6-x-1985, *Farrant*, UNSW 18606; Port Macquarie (31°27′S, 151°26′E), 21-xi-1972, *Coveny* 4737, NSW; Broughton I., 15m, 28-iv-1985, *Farrant*, UNSW 18016; Fairlight, 1-2m, 20-v-1986, *Farrant*, UNSW 18372; Clovelly, 1-3m, 28-ii-1985, *Farrant*, UNSW 17656; Long Bay, June 1915, *Lucas*, NSW; Steamers Beach, 11-vii-1979, *King and Kertesz*, UNSW 15363. Victoria: Brighton, Jan. 1900, *Lucas*, NSW.

COMPARISON WITH *DILOPHUS* SPECIES IN ADJACENT REGIONS

Species concepts in the genus *Dilophus* are unsatisfactory. Womersley (1987) has reduced the number of species on the southern Australian coast from eleven (Womersley, 1967) to seven: *D. marginatus*, *D. robustus* (J. Agardh) Womersley, *D. angustus* J. Agardh, *D. tener* J. Agardh, *D. crinitus* J. Agardh, *D. fastigiatus* (Sonder) J. Agardh, and *D. gunnianus* J. Agardh. Two of the species of *Dilophus* recorded for northern Australia, *D. intermedius* and *D. marginatus* (Lewis, 1985), are found in southern Queensland and at Lord Howe Island (Allender and Kraft, 1983).

Lobospira Areschoug

Growth apical from short rows of cells at the apices of the axes and laterals (not in the determinate laterals). **Thalli** with recurved attaching lower lateral branches, upper free branches twisted and bearing bicuspid determinate laterals; midrib present, especially in the lower half of branches; sporangia scattered and sunken in the thallus.

The monotypic genus *Lobospira* is easily distinguished from all other genera by its distinctive morphology. Growth is from a cluster of apical cells (Edelstein and Womersley, 1975).

Lobospira bicuspidata Areschoug, 1854:364. Edelstein and Womersley, 1975:149; Womersley, 1987:214.

Thalli 10-25cm long; fronds 1-2mm wide (Fig. 8**A**,**B**).

Seasonality: only one collection from New South Wales, that of Lucas in January 1910.

Australian distribution: southern Australia (from Nickol Bay, Western Australia to Eden, New South Wales) (Womersley, 1987); found from just below LWM to a depth of 13m; only collected once in New South Wales (Lucas, Eden, Jan. 1910, 10 specimens in NSW) so possibly drift from the south; not collected in this survey.

Selected specimens examined: New South Wales: Eden, Jan. 1910, *Lucas*, NSW. Victoria: Point Lonsdale, 26-ii-1979, *King*, UNSW 16018; Sandringham, Jan. 1900, *Lucas*, NSW. South Australia: Port MacDonnell, 13-iv-1975, *Harada* R2666, NSW.

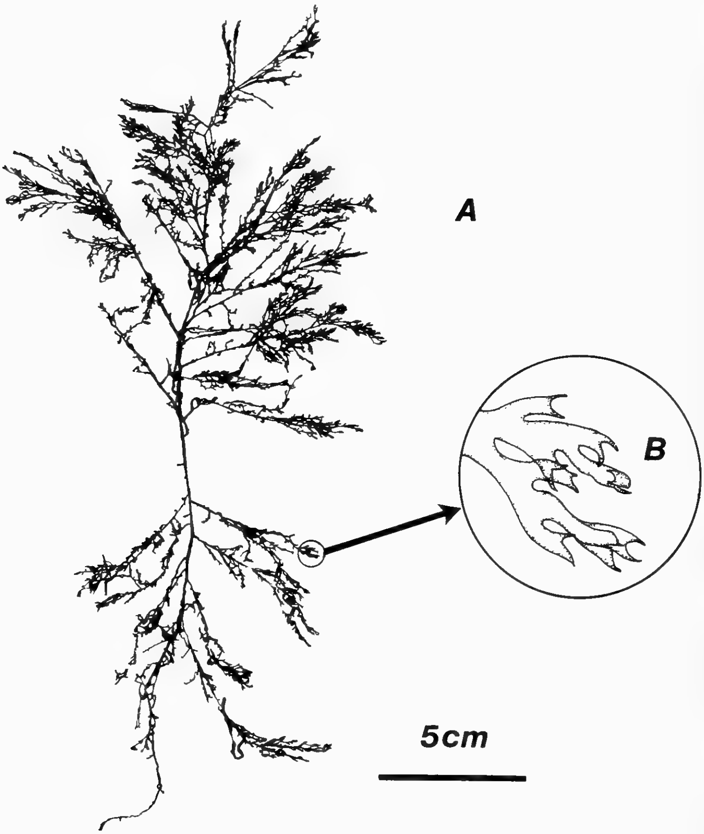


Fig. 8. Lobospira bicuspidata: (**A**) habit (Eden, Jan. 1910, A. H. S. Lucas), (**B**) frond apex.

Dictyopteris Lamouroux

Growth from a small group of initials generally in a slight apical depression. **Thalli** erect, smooth, flattened, membranous to coarse, mostly delicate; fronds with a conspicuous midrib, branches arising from the midrib or margins; hair clusters and reproductive organs on both surfaces; in section consisting of an inner zone of more or less cuboidal to angular colourless cells, and an outer layer of small cuboidal pigmented cells.

Dictyopteris arostichoides is the only species of *Dictyopteris* on the New South Wales coast.

Dictyopteris acrostichoides (J. Agardh) Boergesen, 1935:36. Womersley 1987:226.

Haliseris acrostichoides J. Agardh, 1882: 133.

Thalli 15-30(-55)cm long, branching often but not always from or near the midrib, with some marginal branching in upper parts; fronds (0.4-)0.8-1.0(-1.5)cm wide (Fig. 9**A**); reflexed lines of hair tufts present, no veinlets; 4(-6) cells thick except in the region of the midrib (Fig. 9**B-D**); sporangia embedded in the cortical layer (Fig. 9**B**,**C**), scattered in two distinct elongate sori, leaving the midrib area and marginal zones sterile (Fig 9**A**); fertile regions of male plants forming irregularly shaped pale patches on

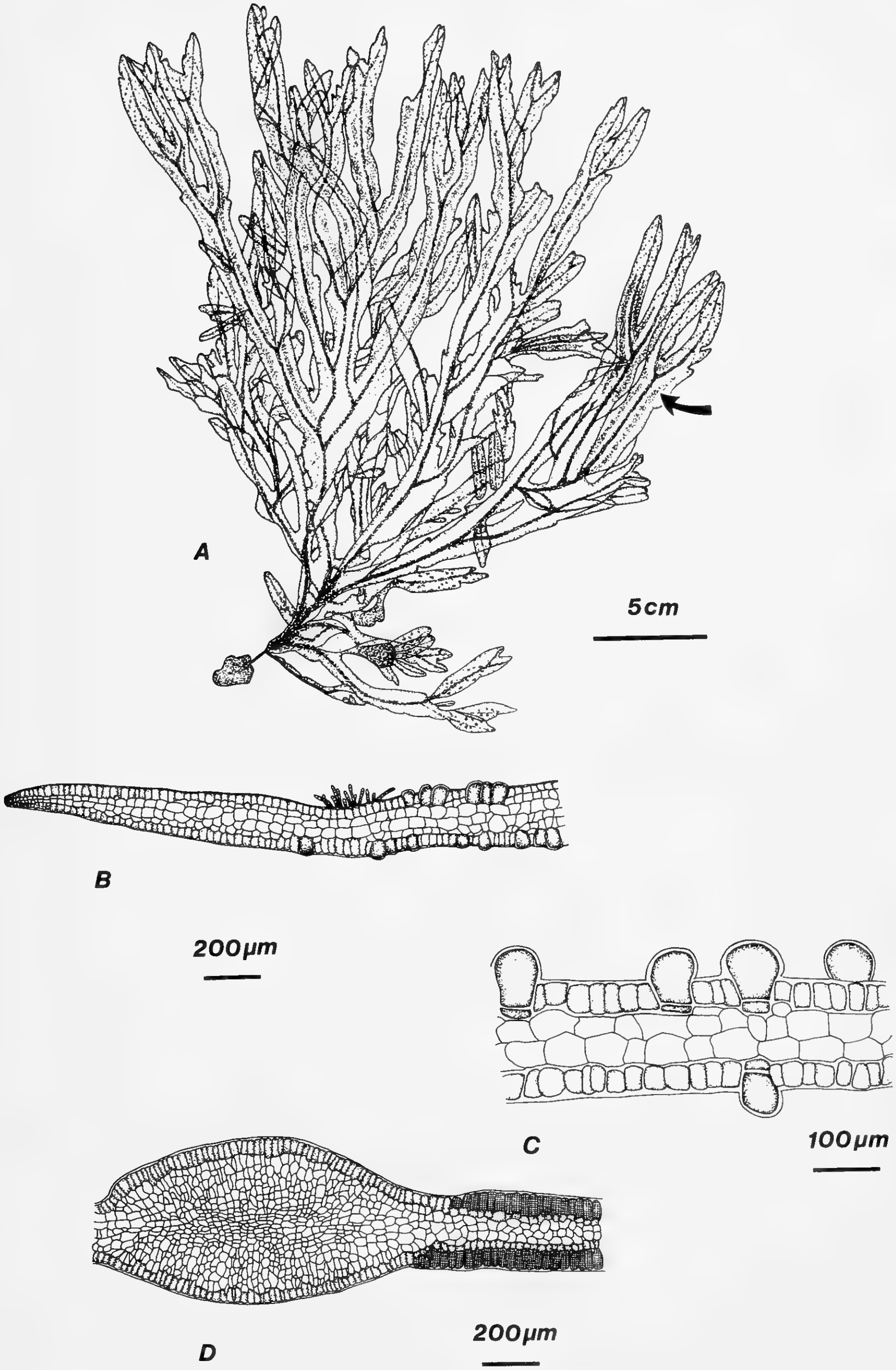


Fig. 9. Dictyopteris acrostichoides: (**A**) habit of sporangial plant, showing longitudinal sori (arrow) (UNSW 17663), (**B**) T.S. of frond showing hair tufts (UNSW 18345), (**C**) T.S. of frond showing sporangia (UNSW 17647), (**D**) T.S. of male frond showing midrib and antheridial sori (UNSW 17647).

the frond wings with antheridial sori sunken in the thallus (Fig. 9**D**); in dried herbarium material male plants difficult to distinguish from sterile plants.

Seasonality: collected in all months of the year; sporangial plants in all months except May and August; male gametophytes (Fig. 9**D**), previously unrecorded, collected in February and September from Sydney Harbour; female plants not found.

Australian distribution: from Warrnambool, Victoria, to Rockingham, Queensland, and along the northern coast of Tasmania (Womersley, 1987); many published records for New South Wales (e.g. Lucas, 1913, 1914; May, 1939; Womersley, 1949), where plants grow in the shallow sublittoral, in sheltered localities on rough water coasts and in bays.

Selected specimens examined: New South Wales: Pottsville Beach, 19-v-1986, *Phillips*, MUCV 2560; Woolgoolga, Jan. 1972, *V. May*, NSW 126974; Crescent Head, LWM, 9-x-1985, *P. and W. Farrant*, UNSW 18652; Camp Cove, 1-2m, 28-ii-1985, *Farrant and Puttock*, UNSW 17647; Lady Jane Beach, 1-3m, 28-ii-1985, *Farrant and Puttock*, UNSW 17663; Mrs Macquarie's Point, 1-2m, 13-ix-1985, *Farrant*, UNSW 18291; Point Piper, July 1899, *Lucas*, NSW; Bare I., 6m, 25-vii-1985, *Farrant*, UNSW 18246; Crookhaven Heads, LWM, 12-iv-1986, *King*, UNSW 18635. Queensland: Noosa, Nov. 1943, *V. May* 989, NSW; Margate, 21-xii-1943, *V. May* 987, NSW; Sandgate, Dec. 1913, *Lucas*, NSW.

COMPARISON WITH *DICTYOPTERIS* SPECIES IN ADJACENT REGIONS

Four species of *Dictyopteris* (*D. australis* (Sonder) Askenasy, *D. gracilis* Womersley, *D. muelleri* (Sonder) Reinbold, and *D. nigricans* Womersley) occur in southern Australia but not New South Wales (Womersley, 1987). There are five species recorded for Lord Howe Island: *D. australis* and *D. plagiogramma* (Montagne) Vickers, both of which have veinlets; *D. repens* (Okamura) Boergesen and *D. delicatula* Lamouroux, distinguished by their small size (and perhaps representing a single species); and *D. crassinervia* (Zanardini) Schmidt distinguished by its unique winged apices (Allender and Kraft, 1983). *Dictyopteris crassinervia*, *D. delicatula* and *D. repens* are also recorded from Queensland (Allender and Kraft, 1983; Ngan and Price, 1979, 1980).

REJECTED SPECIES RECORDS

Dictyopteris australis (Sonder) Askenasy: Allender and Kraft (1983) stated that *D. australis* 'is now known to occur generally around Australia.' There are in fact no records for Victoria or New South Wales though the species occurs in South Australia, Western Australia, Queensland (Womersley, 1987) and at Lord Howe Island (Allender and Kraft, 1983). The species is similar to *D. acrostichoides*, but is easily distinguished by the presence of fine lateral veins and by the distribution of the sori and associated hair tufts in reflexed lines. The frond wings of *D. australis* are generally distromatic rather than of four or more cells as in *D. acrostichoides*.

Dictyopteris muelleri (Sonder) Reinbold: Harvey's specimen of *D. muelleri* (NSW 140374, Harv. Alg. Austr. Exsic. n. 87, 1855) was referred to by May (1939) and on that basis Womersley (1987) recorded *D. muelleri* for New South Wales. The specimen has no collecting locality. Harvey (1860) listed Port Jackson, New South Wales as a collecting locality but he stated that the species was rare on the east coast. The species record for New South Wales therefore has no reliable herbarium voucher specimen and the species has not been recorded otherwise from New South Wales. *Dictyopteris muelleri* has a southern Australian distribution and is easily distinguished from *Dictyopteris acrostichoides* by the evenly scattered hair tufts which are not arranged in reflexed lines; fertile *D. muelleri* material is easily recognized, since sporangia, oogonia and antheridial sori occur in broad bands across the thallus and the midrib and marginal regions are sterile (J. Phillips, *pers. comm.*).

Dictyopteris plagiogramma (Montagne) Vickers: although Allender and Kraft (1983) recorded this species from the Coffs Harbour region of New South Wales, there is no herbarium voucher specimen (A. Miller and G. Kraft, *pers. comm.*). *Dictyopteris plagiogramma* occurs at Lord Howe Island (Allender and Kraft, 1983) and in northern Australia (Lewis, 1985). It is distinguished from *D. acrostichoides* by the presence of fine lateral veins and by the arrangement of hair tufts in single longitudinal rows on each side of the midrib.

Dictyopteris woodwardii (R. Brown ex Turner) Schmidt: was recorded for Ballina by Sonder (1871) as *Halyseris polypoidioides* var. *woodwardia*. This was based on a specimen in MEL (584114) which has been annotated by B. M. Allender (12-vii-1981) as *D. acrostichoides*. *Dictyopteris woodwardii* is otherwise recorded for northern Australia (Lewis, 1985). The species is distinguished from *D. acrostichoides* by having frond margins fringed with minute spine-like teeth.

Spatoglossum Kuetzing

Growth initiated by a group of apical cells. **Thalli** broad, complanate; fronds branching irregularly, hair tufts scattered; sporangia scattered and sunken in the frond surface.

Spatoglossum macrodontum is the only species of the genus in New South Wales.

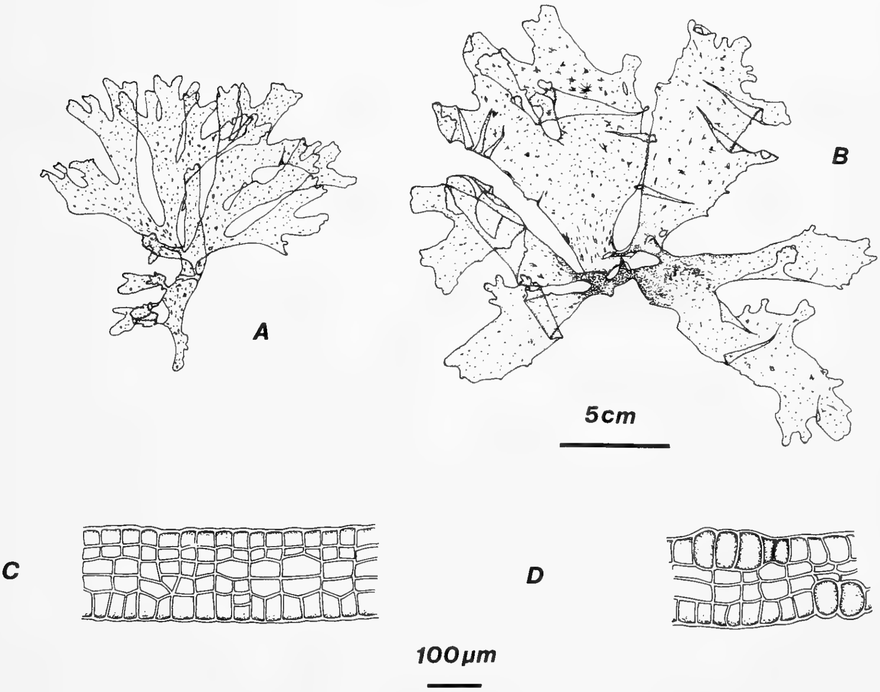


Fig. 10. Spatoglossum macrodontum: (**A**) habit of small plant (UNSW 17740), (**B**) habit of large broad plant (UNSW 18714), (**C**) T.S. frond (UNSW 18251), (**D**), section through sporangia (UNSW 17791).

Spatoglossum macrodontum J. Agardh, 1882:113. Allender and Kraft, 1983:100.

Thalli 10-35cm long, medium to dark brown (drying to a greenish-brown colour); fronds 3-8cm wide, complanate; branching irregular with unequal development of dichotomies, margins smooth in young plants (Fig. 10**A**) but irregular to dentate in older, larger plants (Fig. 10**B**); 4-6 cells thick and cells arranged irregularly (Fig. 10**C**); sporangia scattered and sunken in the frond surface (Fig. 10**D**).

Seasonality: collected in all months except February, but seasonally abundant, with young plants present at the end of winter and early spring; sporangial plants collected in most months in this study and spent male gametangial plants in June, July and August.

Australian distribution: Jervis Bay, New South Wales, north to Queensland and the Northern Territory, and at Lord Howe Island (Allender and Kraft, 1983; Lucas, 1909, 1914; May, 1939); locally abundant in the shallow sublittoral.

Selected specimens examined: New South Wales: Port Stephens, June 1909, *Lucas*, NSW 140350; Port Stephens, 0-2m, 11-x-1985, *P. and W. Farrant*, UNSW 18714; Vaucluse, 1m, 21-xi-1985, *Farrant*, UNSW 18577; Mrs Macquarie's Point, 2-3m, 29-vii-1985, *Farrant*, UNSW 18251; Mrs Macquarie's Point, 2m, 27-vi-1985, *Farrant and Puttock*, UNSW 18208; Jervis Bay, 9-x-1941, *V. May* 983, NSW. Queensland: Magnetic I., 15-v-1987, *Phillips*, MUCV 2565; Redcliffe, 5-vi-1980, *Alderslade* R3988, NSW.

COMPARISON WITH *SPATOGLOSSUM* SPECIES IN ADJACENT REGIONS

Spatoglossum macrodontum as well as two other species, *S. asperum* J. Agardh and *S. shroederi* (Mertens) J. Agardh, have been recorded from northern Australia (Lewis, 1985). *Spatoglossum macrodontum* is the only species found at Lord Howe Island (Allender and Kraft, 1983). *Spatoglossum macrodontum* appears to be closely related to *S. australasicum* Kuetzing from South Australia, but there is little material (and no fertile material) of *S. australasicum* available for comparison (Womersley, 1987).

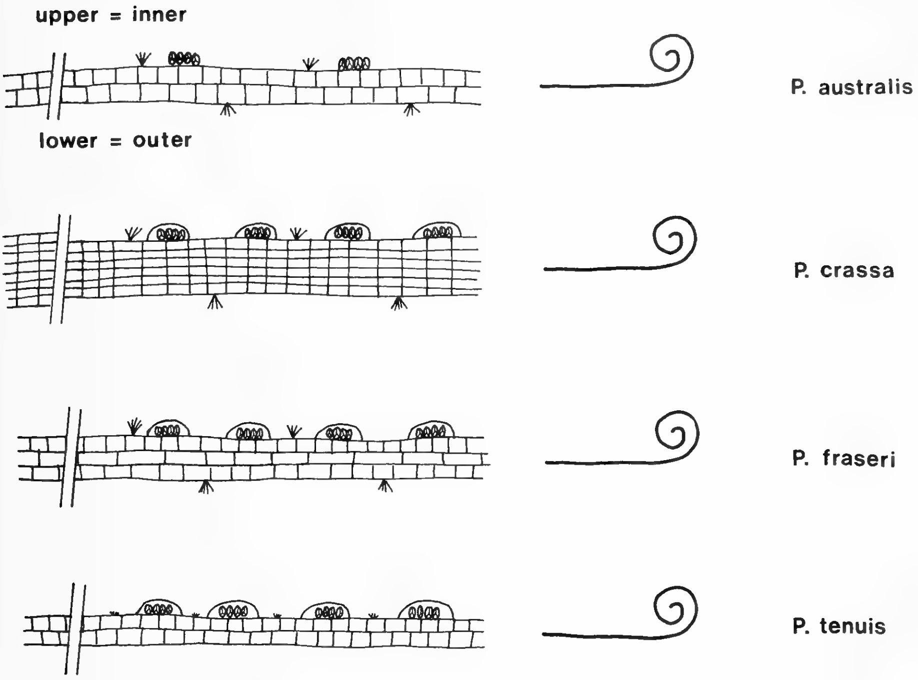
Padina Adanson

Growth from a marginal row of apical cells. **Thalli** flabellate with inrolled margins, calcified to various degrees.

Four species of *Padina* occur on the New South Wales coast: *Padina australis* which is not common, *P. crassa*, *P. fraseri*, and *P. tenuis*. The four species, especially the last two, are difficult to separate without sectioning and/or reproductive material (Fig. 11).

KEY TO THE SPECIES OF *PADINA* IN NEW SOUTH WALES

1. Thallus 2 cells thick throughout 2
1.* Thallus more than 2 cells thick except near the apex 3
2. Sporangia on upper surface in concentric lines bordered on each side by hair bands that alternate on upper and lower surfaces; sporangial regions separated from each other by sterile zones .... *P. australis*
2.* Sporangia on upper surface in concentric lines bordered on each side by hair bands that are only on the upper surface; sporangial regions not separated from each other by sterile zones .... *P. tenuis*
3. Thallus 3 cells thick throughout .... *P. fraseri*
3.* Thallus 6-10 cells thick .... *P. crassa*



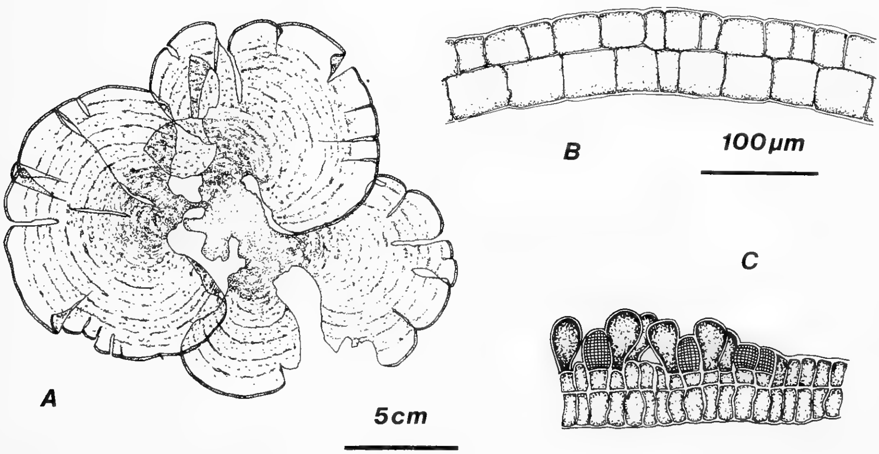


Fig. 11 (above). Diagram showing distribution of hairs and sori on New South Wales species of *Padina* (not to scale).
Fig. 12 (below). *Padina australis:* (**A**) habit of gametangial plant (UNSW 17705), (**B**) T.S. top of frond (UNSW 17705), (**C**) section through female and male gametangia (UNSW 17705).

Padina australis Hauck, 1887:44. Allender and Kraft, 1983:85.

Thalli 6-10cm long; fronds 4-12cm wide (Fig. 12**A**), with conspicuous hairs on both surfaces, hair lines 1-1.5mm apart; distromatic throughout (Fig. 12**B**); gametangial plants monoecious, with female and male gametangia in mixed sori (Fig. 12**C**) on the upper (inner) frond surface, alternating fertile and sterile zones.

Seasonality: collected in February and March only, from Church Point, Pittwater; gametangial plants present in both collections; no sporangial plants found.

Australian distribution: reported from Lord Howe Island, and in mainland Australia from the central New South Wales coast to the Northern Territory (Allender and Kraft, 1983); in this survey found on rocks just below low water mark in a very sheltered part of the estuary.

Selected specimens examined: New South Wales: Lord Howe I., 14-v-1977, *Kraft*, MELU A037276; Lord Howe I., 16-xii-1986, *Kraft and Millar*, MELU A037275; Church Point Pittwater, LWM, 17-iii-1985, *Farrant*, UNSW 17705.

Padina crassa Yamada, 1931:67. Allender and Kraft, 1983:87.

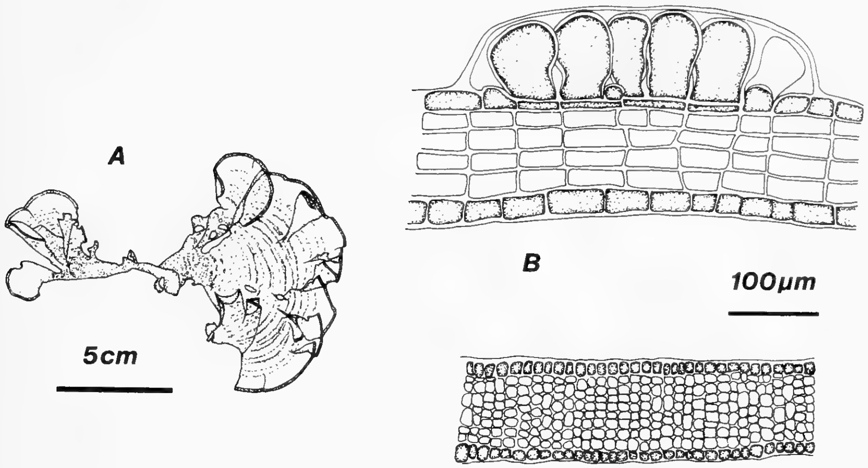
Thalli 6-16cm long; fronds 3-10cm wide (Fig. 13**A**), hairs conspicuous, in alternating rows on each frond surface, (2-)4-5(-7.5)mm apart; fronds 6-8(-10) cells thick except at the apex (Fig. 13**B**,**C**); sporangial sori indusiate (Fig. 13**B**) and mainly on the upper (inner) side of the frond (occasionally on both surfaces), fertile zones not separated by sterile zones.

Padina crassa specimens from the New South Wales mainland coast agree with Allender and Kraft's (1983) Lord Howe Island material in that they have no sterile zones, have the same seasonality and indusiate sori. The mainland material has hairs on both frond surfaces whereas the Lord Howe Island plants have them only on the upper surfaces.

Allender and Kraft (1983) stated that 'there is little if any significant difference between . . . *P. gymnospora* and *P. crassa* from the eastern and southern Pacific'. Womersley (1987) recorded *P. gymnospora* (Kuetzing) Sonder in southern Australia, noting that it has a distribution extending into warm temperate waters on both eastern and western coasts of Australia. He noted however that, according to Allender and Kraft (1983), *P. crassa* from Lord Howe Island has sori on the outer (lower) surface only, whereas in *P. gymnospora* the sori are mainly (but not only) on the upper surface.

Allender and Kraft (1983) attempted to clarify the confusion which 'surrounds the terminology used to describe the morphology and anatomy of the species' of *Padina* and correctly defined the use of the terms inner and outer, the inner being the 'side towards which the marginal curl is directed'. In their descriptions of *P. australis*, *P. crassa* and *P. tenuis* Allender and Kraft stated that the sporangial sori are located on the outer frond surfaces, and in their fig. 6 the outer surface is correctly referred to as the 'upper' surface. We have examined fertile specimens of all these species from Lord Howe Island (MELU A037276, MELU A037275, MELU GK9560, MELU A037274) and of *P. fraseri* from Victoria (MELU 4290), and the sori in all cases occur on the surface to which the marginal roll is directed, i.e., the inner surfaces. The descriptions of these species in Allender and Kraft (1983) should therefore read sporangial sori on inner frond surface rather than outer. The inner surface is then equivalent to the upper surface in the terminology used by Womersley (1987).

The material from New South Wales and Lord Howe Island thus differs from *Padina gymnospora* in that it has indusiate sori whereas *P. gymnospora* has essentially non-indusiate sori. *Padina gymnospora* and the New South Wales specimens have hairs on both surfaces whereas the Lord Howe Island species has hairs on the upper surface only. The



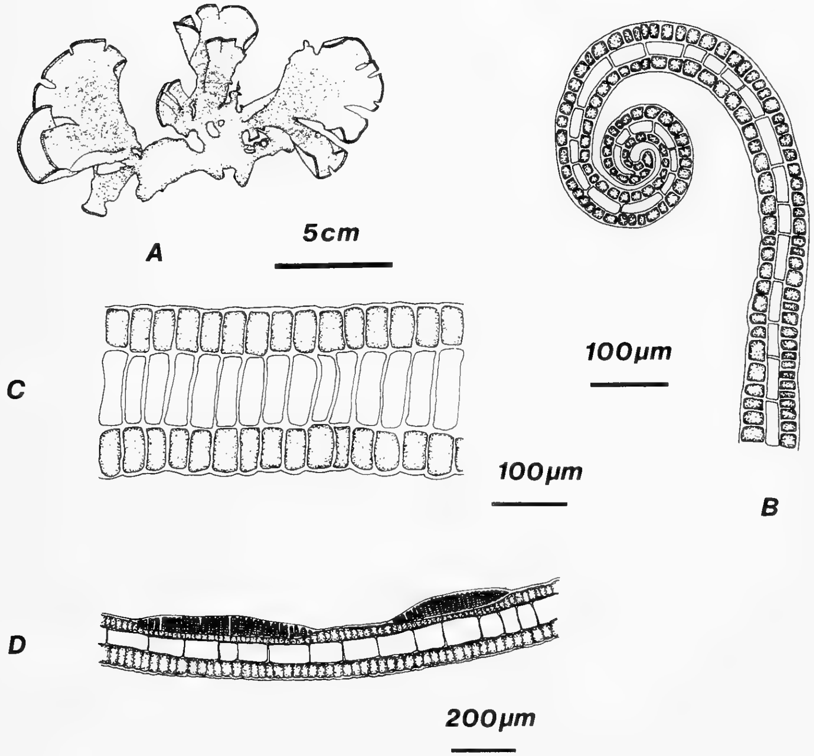


Fig. 13 (above). *Padina crassa:* (**A**) habit (UNSW 18041), (**B**) sporangial sorus (UNSW 17766), (**C**) base of frond (UNSW 18803).
Fig. 14 (below). *Padina fraseri:* (**A**) habit (UNSW 18685), (**B**) L.S. apex (UNSW 18002), (**C**) T.S. base of frond (UNSW 18685), (**D**) section through male sorus (UNSW 17665).

relationship between these two taxa deserves attention; examination of type specimens may show that the two are not distinct.

Seasonality: absent in the winter months; sporangial plants collected in the warmer months (King and Farrant, 1987); no gametangial plants collected.

Australian distribution: Lord Howe Island (Allender and Kraft, 1983) and in Queensland (UNSW 16036); in this survey north to Hastings Point and south to Jervis Bay; found in the shallow upper subtidal, on the open coast and in bays and estuaries.

Selected specimens examined: New South Wales: Hastings Point, 19-v-1986, *Phillips*, MUCV 2563; Coffs Harbour, 2-4m, 4-x-1981, *Farrant*, UNSW 18041; South West Rocks, LWM, 9-x-1985, *P. and W. Farrant*, UNSW 18637; Lord Howe I., 9-xii-1978, *Kraft and Ricker*, MELU GK 9560; Fairlight, 1m, 29-i-1986, *Farrant*, UNSW 18829; Vaucluse, 1m, 18-iv-1985, *Farrant and Puttock*, UNSW 17790; Jervis Bay, LWM, 18-iii-1985, *King*, UNSW 17709. Queensland: Noosa, 4-xii-1976, *King and Kertesz*, UNSW 16036.

Padina fraseri (Greville) Greville, 1830, synop.:xliv. Womersley, 1987:217.

Thalli 6-9.5cm long, often distinctly crinkled; fronds 3-7.5cm wide (Fig. 14**A**), with alternate concentric hair lines on both sides of the fronds, (2-)4(-7)mm apart; 3 cells thick almost to the apex (Fig. 14**B**), with central (medullary) cells larger than cortical cells (Fig. 14**B-D**); sporangial sori indusiate, no sterile zones between hair lines; male gametangial plants with indusiate antheridial sori (Fig. 14**D**).

Padina pavonica (Linnaeus) Lamouroux has been recorded for Port Jackson, New South Wales (May, 1939) and generally for New South Wales and Lord Howe Island (Lucas, 1909, 1914, 1935). This species differs from *P. fraseri* in not having the central (medullary) cells longer than the outer cells (Allender and Kraft, 1983: fig. 6D,F). The records of *P. pavonica* for New South Wales probably mostly refer to *P. fraseri*, since the NSW specimens that have been examined in the present study, and which are 3 cells thick, have longer central cells and a crinkled thallus, and therefore appear to belong to *P. fraseri*.

Seasonality: sporophytic plants collected especially in the warmer months, and male plants, the first sexual plants to be recorded for the species, collected in February.

Australian distribution: recorded from south-eastern Australia from Warrnambool, Victoria, to the mid north New South Wales coast (Womersley, 1987); grows at and just below low water mark, on rocky open coasts.

Selected specimens examined: New South Wales: Crescent Head, LWM, 9-x-1985, *P. and W. Farrant*, UNSW 18649; Seal Rocks, 0-2m, 10-x-1985; *P. and W. Farrant*, UNSW 18680; Lady Jane Beach, 1-3m, 28-ii-1985, *Farrant and Puttock*, UNSW 17665; Wollongong, Jan. 1912, *Lucas*, NSW; Kiama, Dec. 1899, *Lucas*, NSW; Crookhaven Heads, LWM, 20-iv-1985, *Farrant*, UNSW 18002; Merimbula, 19-viii-1987, *D. May* MUCV 2575. Victoria: Barwon Heads, 7-ii-1969, *Ducker*, MELU 4290; Apollo Bay (38°46′S, 143°44′E), 23-i-1967, *Womersley*, NSW ex ADU A31758.

Padina tenuis Bory, 1827:590. Womersley and Bailey, 1970: 292; Allender and Kraft, 1983:83.

Thalli 6-18cm long; fronds 3-12cm wide (Fig. 15**A**), without conspicuous hairs below the first hair line, hair scar lines (1.5-)3-4(-6)mm apart; fronds distromatic throughout (Fig. 15**B**,**C**); sporangial sori indusiate (Fig. 15**B**) or have the remains of an indusium, fertile zones not separated by sterile zones.

The New South Wales specimens of *Padina tenuis* agree well with Allender and Kraft's (1983) description of the species for Lord Howe Island and the southern Great

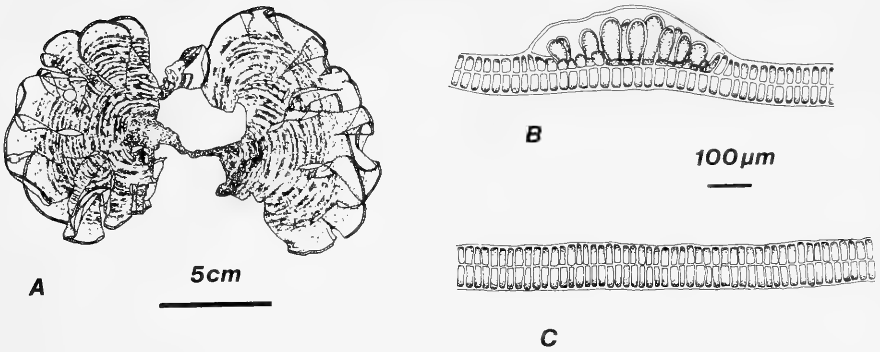


Fig. 15. Padina tenuis: (**A**) habit (UNSW 18068), (**B**) T.S. base of frond through sporangial sorus (UNSW 18583), (**C**) T.S. base of frond (UNSW 18583).

Barrier Reef, except that their material has non-indusiate sori and the fronds are 2-3 cells at the base. Almost all New South Wales specimens have indusiate sori and are 2 cells thick throughout. Lord Howe Island material examined during the present study (MELU A037274) showed that the remains of indusia were present. The New South Wales and Lord Howe Island specimens therefore appear to belong to the same taxon, *P. tenuis*, although examination of type material would be required to confirm this.

Seasonality: collected in all months, sporangial plants in all months except July, August and October; no gametophytic plants present.

Australian distribution: recorded for Lord Howe Island and the southern Great Barrier Reef (Allender and Kraft, 1983) but not reported previously for the mainland coast of New South Wales; grows from a depth of several metres to 16m, on both sheltered and open coast shores.

Selected specimens examined: New South Wales: Pottsville Beach, 19-v-1986, *Phillips*, MUCV 2559; NW Solitary I., 10-16m, 6-x-1985, *Farrant*, UNSW 18608; Lord Howe I., i-xii-1978, *Kraft and Ricker*, MELU A037274 (=GK 9405); Broughton I., 15m, 28-iv-1985, *Farrant*, UNSW 18015; Barrenjoey, 15m, 23-iii-1985, *Farrant*, UNSW 17728; Mrs Macquarie's Point, 1-2m, 26-iii-1986, *Farrant and Puttock*, UNSW 18341; Long Bay, Apr. 1900, *Lucas*, NSW.

COMPARISON WITH *PADINA* SPECIES IN ADJACENT REGIONS

Padina australis, *P. crassa* and *P. tenuis* occur at Lord Howe Island (Allender and Kraft, 1983). *Padina boergesenii* Allender and Kraft was described on the basis of Lord Howe Island material (Allender and Kraft, 1983). It is rare and has not been recorded for the New South Wales mainland coast, although Allender and Kraft (1983) suggest that it probably occurs in Queensland. *Padina tetrastromatica* Hauck, which occurs in Queensland, is similar to *P. fraseri* except that it becomes 4-layered in older thallus parts (Allender and Kraft, 1983: fig. 6E). *Padina fraseri* is the only species of *Padina* for most of the southern Australian coast, with three other species now recognized from the western end of that region: *P. elegans* Koh *ex* Womersley, *P. gymnospora* (Kuetzing) Sonder, and *P. sanctae-crucis* Boergesen (Womersley, 1987).

Distromium Levring

Growth from a marginal row of apical cells. **Thalli** two cells thick throughout (3 cells thick at hairs).

There is only one species of *Distromium* (*D. flabellatum*) in New South Wales. The plants are relatively small compared with those reported from southern Australia, and no fertile plants have been seen in the New South Wales material. Therefore the identification to specific level is provisional since fertile material is required to establish its relationship with *D. skottsbergii* Levring (Womersley, 1967; Lindauer *et al.*, 1961).

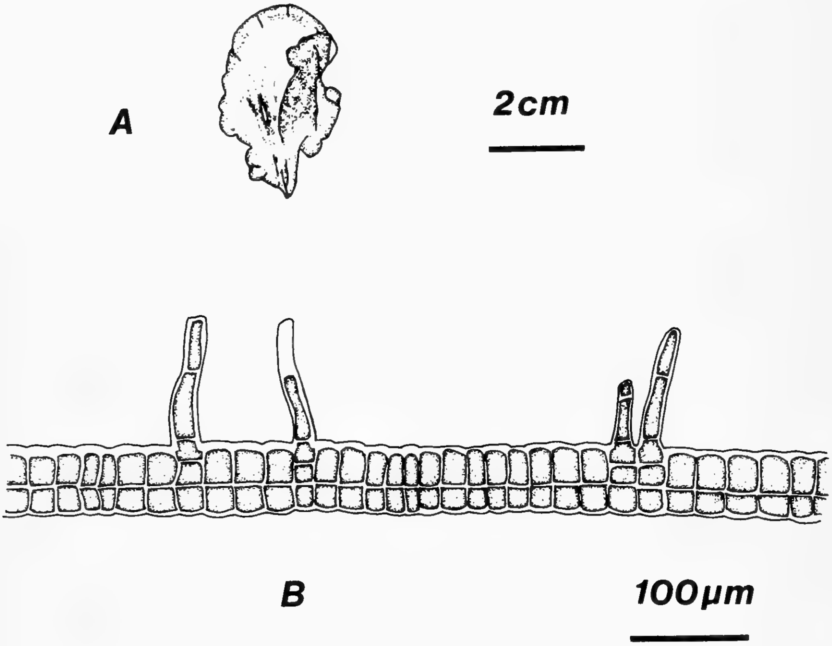


Fig. 16. Distromium flabellatum: (**A**) habit (UNSW 18849), (**B**) section of frond (UNSW 18873).

Distromium flabellatum Womersley, 1967:218. Womersley, 1987:230.

Thalli 2-3cm long, slightly blue-green when seen *in situ*; frond(s) 2-3cm wide (Fig. 16**A**), flabellate; hairs borne singly (Fig. 16**B**).

Seasonality: collected in this study in April and September; no reproductive plants found.

Australian distribution: recorded from 7 Mile Beach, north of Dongara, Western Australia and along the southern Australian coast to Deal I. in Bass Strait (Womersley, 1987); now tentatively recorded for New South Wales; in this study collected at only one locality (Fairlight, Sydney Harbour) on the vertical face of a rocky reef at 4-5m depth; may be more widespread, but is easily overlooked because of its superficial similarity to young *Zonaria diesingiana* plants, which however differ by being 6-8 cells thick.

Selected specimens examined: New South Wales: Fairlight, 5m, 29-iv-1986, *Farrant*, UNSW 18849; Fairlight, 4m, 25-ix-1986, *Farrant*, UNSW 18873 (wet material only); South Australia: Aldinga (35°20′S, 138°28′E), 17-ix-1966, *Womersley*, NSW ex ADU A30711.

COMPARISON WITH *DISTROMIUM* SPECIES IN ADJACENT REGIONS

Distromium flabellatum is distinguished from the Lord Howe Island species, *D. didymothrix* Allender and Kraft, by having hairs borne singly, rather than in pairs derived from a single cell (Allender and Kraft, 1983). There are two species of *Distromium* in southern Australia: *D. flabellatum* and *D. multifidum* Womersley. The latter has linear, subdichotomous branches with small sporangial sori in the upper concave parts; the thallus lacks prominent zones of hairs which the larger southern Australian *D. flabellatum* plants have (Womersley, 1987).

Lobophora J. Agardh

Growth from a marginal row of apical cells. **Thalli** flabellate or irregularly lobed, erect or prostrate; fronds in section having medullary cells in regular tiers, with the central layer of cells larger.

One species, *Lobophora variegata*, has been recorded for New South Wales.

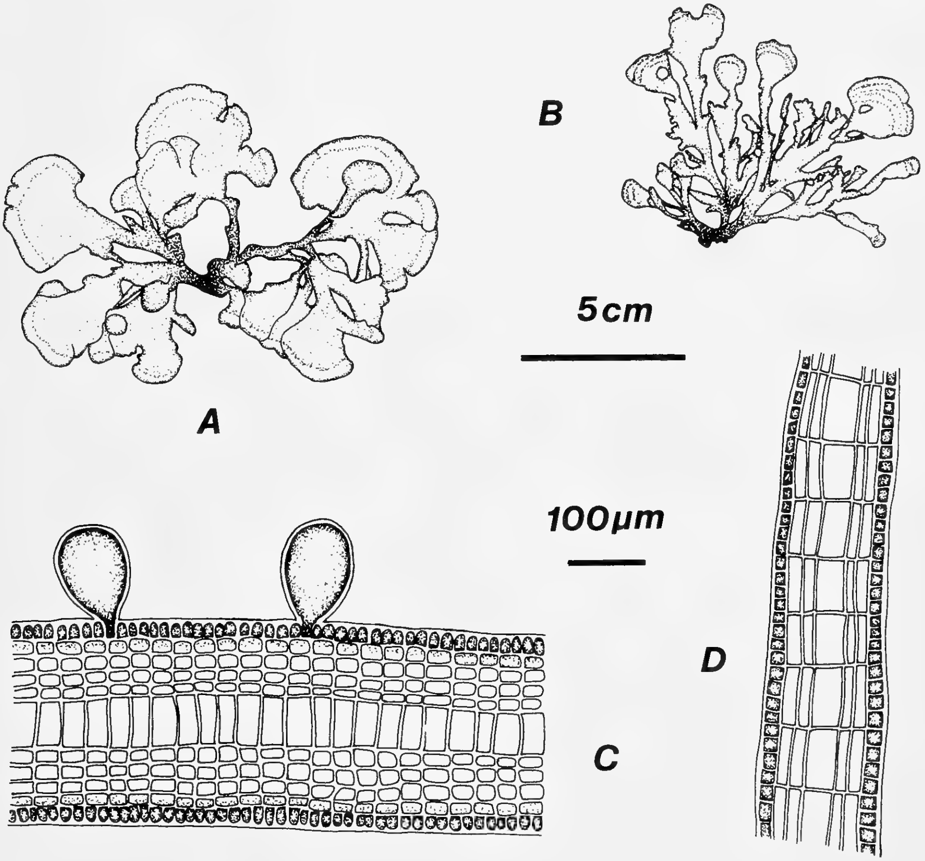


Fig. 17. Lobophora variegata: (**A**) habit of broad erect form (UNSW 18018), (**B**) habit of narrow form (UNSW 17637), (**C**) T.S. of sporangial frond (UNSW 18029), (**D**) L.S. frond (UNSW 18018).

Lobophora variegata (Lamouroux) Womersley, 1967:221. Allender and Kraft, 1983:81.
Gymnosorus variegatus (Lamouroux) J. Agardh 1894:11;
Pocockiella variegata (Lamouroux) Papenfuss 1943:467

Thalli 3-11cm long; fronds 3-6cm wide (Fig. 17**A**,**B**); in transverse section the medulla usually 9 cells thick (Fig. 17**C**), less near the apex (Fig. 17**D**), cells arranged in regular tiers with the central cells larger than the outer cells; sporangia in isolated sori on the fronds.

Young *Lobophora variegata* plants may be confused with young *Zonaria diesingiana* plants, but the latter lack the central layer of larger medullary cells.

Seasonality: sporangial plants collected in all months; gametangial plants not present in collections.

Australian distribution: tropical and temperate coasts of Australia (Womersley, 1987), with numerous records for New South Wales and Lord Howe Island (May, 1939; Lucas, 1914, 1935; Allender and Kraft, 1983; Lindauer *et al.*, 1961; Sonder, 1880); grows on rocky substrata in the subtidal to at least 25m, and common in kelp communities.

Selected specimens examined: New South Wales: Coffs Harbour, 1-2m, 8-x-1985, *P. and W. Farrant*, UNSW 18623; Broughton I., 28-iv-1985, *Farrant*, UNSW 18029; Lord Howe I., Sep. 1908, *Dun and Hedley*, NSW 140443; Long Reef, 12-viii-1974, *Harada* R1269, NSW; Fairlight, 1-3m, 14-v-1985, *Farrant*, UNSW 18054; Dobroyd, 10m, 24-ix-1985, *Farrant*, UNSW 18533; Jervis Bay, LWM, 18-iii-1985, *King*, UNSW 17710. Queensland: Magnetic I., 13-v-1987, *Phillips*, MUCV 2568; Caloundra, Jan. 1909, *Lucas*, NSW 140438; Moreton Bay, Dec. 1913, *Lucas*, NSW 140437.

Zonaria C. Agardh

Growth from a marginal row of apical cells. **Thalli** with fronds in section having moderately distinct cortex and medulla, with medullary cells arranged in vertical tiers and cortical cells mostly paired to each medullary cell; sporangia with 8 aplanospores.

There are three species of *Zonaria* in New South Wales, *Z. diesingiana*, *Z. crenata* and *Z. angustata*. The New South Wales specimens formerly referred to *Zonaria sinclairii* Hooker and Harvey are now placed in *Homoeostrichus* (see below). The taxon referred to as '*Zonaria* sp.' in King and Farrant (1987) is *Homoeostrichus olsenii*.

KEY TO THE SPECIES OF *ZONARIA* IN NEW SOUTH WALES

1.	Thallus narrow 2-4mm wide, linear, 10 cells thick, sporangial sori lacking cellular paraphyses	*Z. angustata*
1.*	Thallus lobed or fan-shaped (to 6cm wide), or linear with cuneate terminal segments (to 2cm wide), 6(-8) cells thick, sporangial sori containing paraphyses	2
2.	Thallus with lobed fronds somewhat denuded below, 6 cells thick, often covered by a network of hydroid	*Z. crenata*
2.*	Thallus lobed or broadly fan-shaped, not denuded below, (6-)8 cells thick, not covered by hydroid	*Z. diesingiana*

Zonaria angustata (Keutzing) Papenfuss, 1952: 170. Womersley, 1987:248.

Thalli 15-17cm long; fronds generally 2-4mm wide, more or less linear (Fig. 18**A**) but occasionally broader (to 20mm) in young plants or at the base; in section 10 cells thick (Fig. 18**B**); sporangial sori scattered on the distal frond surfaces, without cellular paraphyses.

Seasonality: New South Wales collections of *Zonaria angustata* made in January and August only.

Australian distribution: from Elliston, South Australia, to Eden in New South Wales and around Tasmania; only two collections from New South Wales, from Eden and Green Cape, from the shallow sublittoral, 1-3m.

Selected specimens examined: New South Wales: Eden, Jan. 1910, *Lucas*, NSW 140420; Green Cape, 1-3m, 17-viii-1987, *D. May*, MUCV 2571. Victoria: Newfield Bay

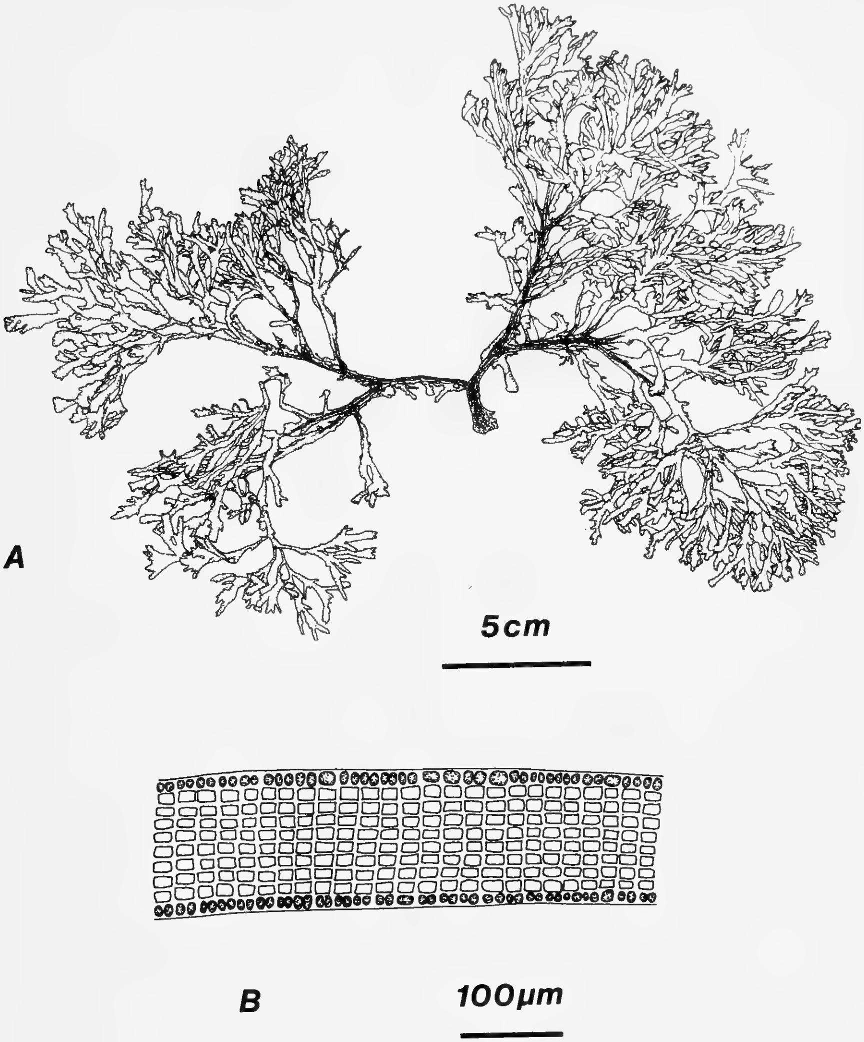


Fig. 18. Zonaria angustata: (**A**) habit (Eden, Jan. 1910, A. H. S. Lucas), (**B**) T.S. frond (MUCV 2571).

(38°36′S, 142°51′E), 10-xii-1969, *Womersley*, NSW ex ADU A3408; Point Lonsdale, 4-xii-1985, *Phillips*, UNSW 19328.

Zonaria crenata J. Agardh 1872:48, 1894:13. Womersley 1987:250.

Thalli 5-15cm long; fronds 1-2cm wide, complanate, broader at the apex and usually denuded at the base (Fig. 19**A**), covered with a network of the hydroid *Scoresbia diadala* Watson (Fig. 19**B**,**C**); 6(-8) cells thick; sporangial sori scattered on the upper parts of the fronds.

Plants of *Z. crenata* are often longer than those of *Z. diesingiana* and have narrower and thinner fronds. They are often distinguished by the hydroid cover, though this feature alone is not sufficient for species identification. New South Wales specimens can

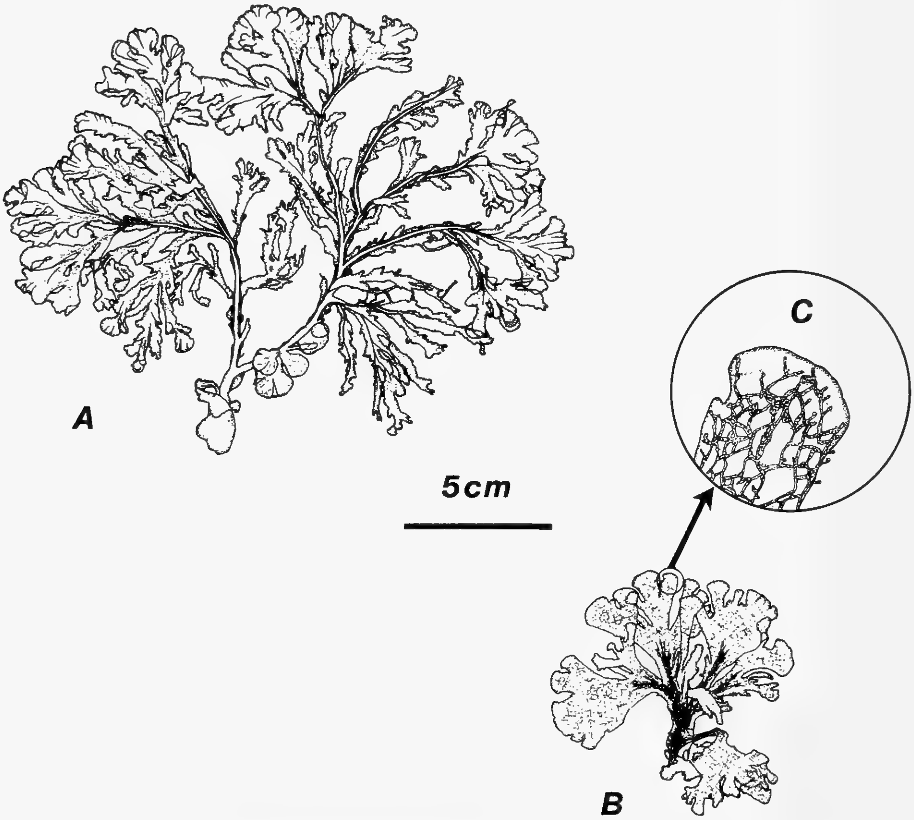


Fig. 19. Zonaria crenata: (**A**) habit (MEL 16937), (**B**) habit of plant doubtfully distinct from *Z. diesingiana* but which is 6 cells thick and has hydroid cover (UNSW 17720), (**C**) frond apex.

be difficult to place and there is considerable overlap between the two species with regard to characters such as frond thickness, frond shape and size, and the degree of hydroid cover. Some *Z. crenata* plants have a form similar to *Z. diesingiana*, with fronds 6 cells thick, complanate with broad tips and denuded lower axes and a cover of hydroid (Fig. 19**B**,**C**). Some Queensland specimens also have the typical *Z. diesingiana* form and yet have a cover of hydroid. The only typical *Z. crenata* specimens from New South Wales seen during this study were those collected from Sydney last century (MEL 16937). The relationship between the two taxa requires elaboration especially as *Z. diesingiana* is not recorded in southern Australia (Womersley, 1987).

Seasonality: not determined.

Australian distribution: from Fremantle, Western Australia, to Southport, Queensland, but rare in New South Wales; specimens examined by Womersley (1987) are either from the drift or from deep water.

Selected specimens examined: New South Wales: Coffs Harbour, 29-viii-1980, *Millar and Kraft*, MELU AM 312 and MELU AM 313; Barrenjoey, 15m, 23-iii-1985, *Farrant*, UNSW 17720; Sydney, ex Herb. Sonder (1812-1881), MEL 16937; Plantation Point, 29-viii-1973, *V. May*, NSW; Green Point Warrah Sanctuary, 17-xii-1972, *Larkum and Martin*, NSW 140433. Queensland: Mooloolaba, 24-i-1944, *V. May* 897, NSW. South Australia: Lefevre Peninsula, ex Herb. *Sonder* (1812-1881), MEL 16936, 16938; Glenelg, 22-viii-1946, *V. May 2235*, NSW; Kingston (36°50′S, 139°51′E), 16-x-1986, *Womersley*, NSW ex ADU A57343.

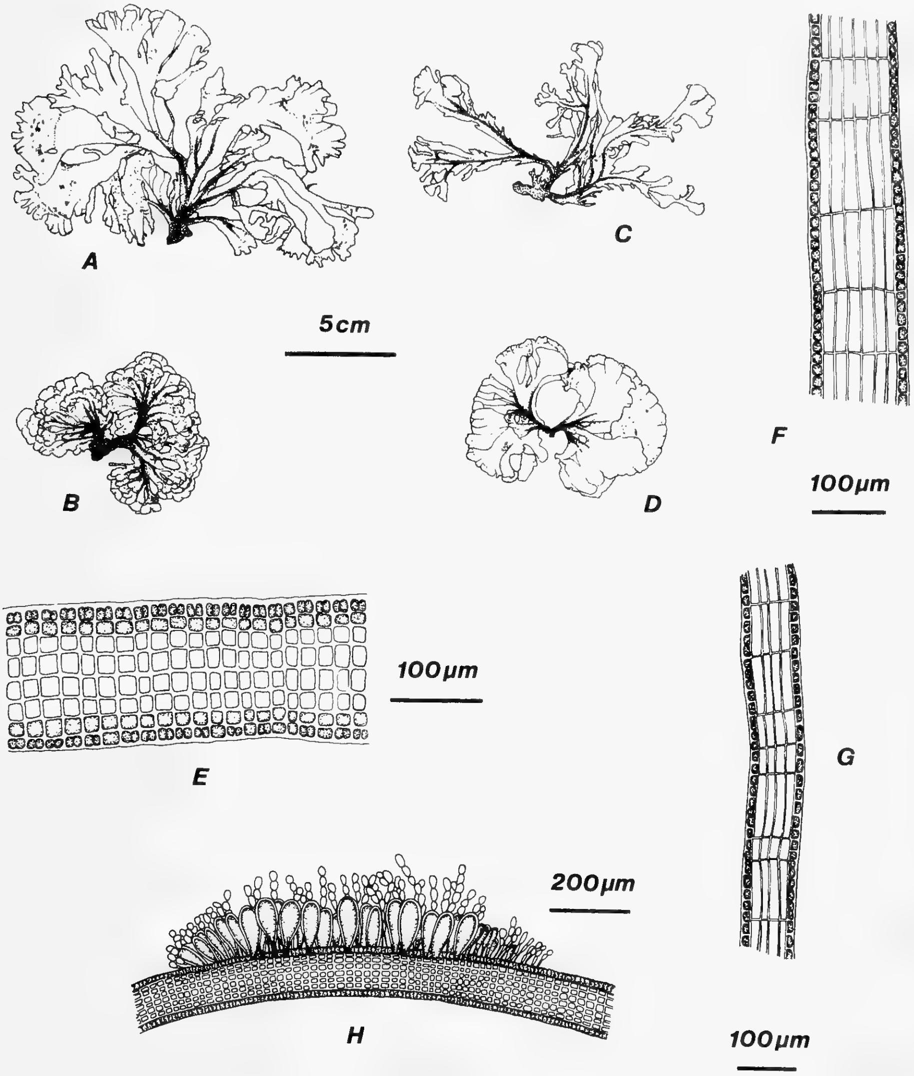


Fig. 20. Zonaria diesingiana: (**A**) habit of broad tall plant (UNSW 18019), (**B**) habit of plant with dense fronds (UNSW 18085), (**C**) UNSW 18292, (**D**) habit of broadly flabellate plant (UNSW 18022), (**E**) T.S. frond (UNSW 18085), (**F**) L.S. frond (UNSW 17755), (**G**) L.S. frond (UNSW 18008), (**H**) T.S. through sporangial sorus (UNSW 18006).

Zonaria diesingiana J. Agardh, 1841:443; 1848:109. Allender and Kraft, 1983:77.

Thalli (1.5-)4-11cm long, variable in habit, from erect to recumbent, often with a slight green or blue iridescence *in situ*; fronds to 1.5-6cm wide, from linear to broad and flabellate (Fig. 20**A-D**), basal fronds often with a stupose central axis, but never completely bare of lateral membranous frond material; (6-)8 cells thick in mid-frond regions (Fig. 20**E-G**); sporangial plants with sori arranged irregularly or in roughly concentric lines, and with sterile paraphyses (Fig. 20**H**).

There are problems in distinguishing *Zonaria diesingiana* from *Z. crenata* in New South Wales (see notes under that species).

Zonaria turneriana has been reported widely from the New South Wales coast (Womersley, 1967; May *et al.*, 1970; May and Larkum, 1981). These records are here recognized as of *Z. diesingiana*.

Seasonality: sporangial plants collected in all months of the year.

Australian distribution: reported from Sydney to Coffs Harbour in New South Wales and Lord Howe Island (Allender and Kraft, 1983); also at Norfolk Island and on the New South Wales coast south to Green Cape; the most abundant dictyotalean alga on the central New South Wales coast (King and Farrant, 1987), at Lord Howe Island (Allender and Kraft, 1983) and in the Coffs Harbour region (A. Millar, *pers. comm.*), in both sheltered and open coast localities in eulittoral rock pools and to depths of 20m; abundance declines markedly with distance south and north of the central New South Wales region.

Selected specimens examined: New South Wales: Hastings Point, 19-v-1986, *Phillips*, MUCV 2561; Coffs Harbour, 1-2m, 8-x-1985, *Farrant*, UNSW 18618; Diamond Head, 0-1m, 10-x-1985, *P. and W. Farrant*, UNSW 18669; Fairlight, 1-2m, 26-xi-1985, *Farrant*, UNSW 18582; Fairlight, 5m, 29-iv-1986, *Farrant*, UNSW 18846; Kiama, July 1899, *Lucas*, NSW; Jervis Bay, LWM, 18-iii-1985, *King*, UNSW 17711; Broulee, 21-viii-1987, *D. May*, MUCV 2574; Malau Bay, 21-viii-1987, *D. May*, MUCV 2569; Barragga Point, LWM, 13-xi-1986, *Farrant*, UNSW 19360. Queensland: Noosa, 4-xii-1976, *King and Kertesz*, UNSW 15313.

COMPARISON WITH *ZONARIA* SPECIES IN ADJACENT REGIONS

Four species are found in southern Australia, *Zonaria angustata*, *Z. crenata*, *Z. spiralis* (J. Agardh) Papenfuss and *Z. turneriana* J. Agardh. *Zonaria spiralis* has a southern distribution from Rottnest Island, Western Australia, to Flinders, Victoria, and has characteristic spirally-twisted branches. *Zonaria turneriana* is found from Geraldton, Western Australia, to Port Phillip Heads, Victoria, Tasmania, and New Zealand. This species has mature fronds that are more or less linear, and 8-10 cells thick, but which are broader than those of *Z. angustata* (2-5[-8]mm). Only *Z. crenata* and *Z. diesingiana* occur in Queensland.

Homoeostrichus J. Agardh

Growth from a marginal row of apical cells. **Thalli** in transverse section having cells of medulla of uniform size and arranged in regular tiers, cells of the cortex mostly unpaired; sporangia with 4 aplanospores.

The genus *Homoeostrichus* was formerly placed within *Zonaria* (Papenfuss, 1944), but has been recently re-established by Womersley (1987). *Homoeostrichus* can be distinguished from *Zonaria* by sporangia with 4 aplanospores, as yet only observed in *H. sinclairii* and *H. olsenii* (*cf.* 8 in *Zonaria*), and by mostly unpaired cortical cells (which are mostly paired in *Zonaria*).

There are two species of *Homoeostrichus* in New South Wales, *H. olsenii* and *H. sinclairii*; both can be difficult to separate from *Zonaria diesingiana*.

KEY TO THE SPECIES OF *HOMOEOSTRICHUS* IN NEW SOUTH WALES

1. Thallus broadly fan-shaped, greyish, 5(-6) cells thick below apex . . . . *H. olsenii*

1.* Thallus with cuneate (wedge-shaped) terminal segments, light brown, denuded below, 6 cells thick except thicker at 'midrib' .... *H. sinclairii*

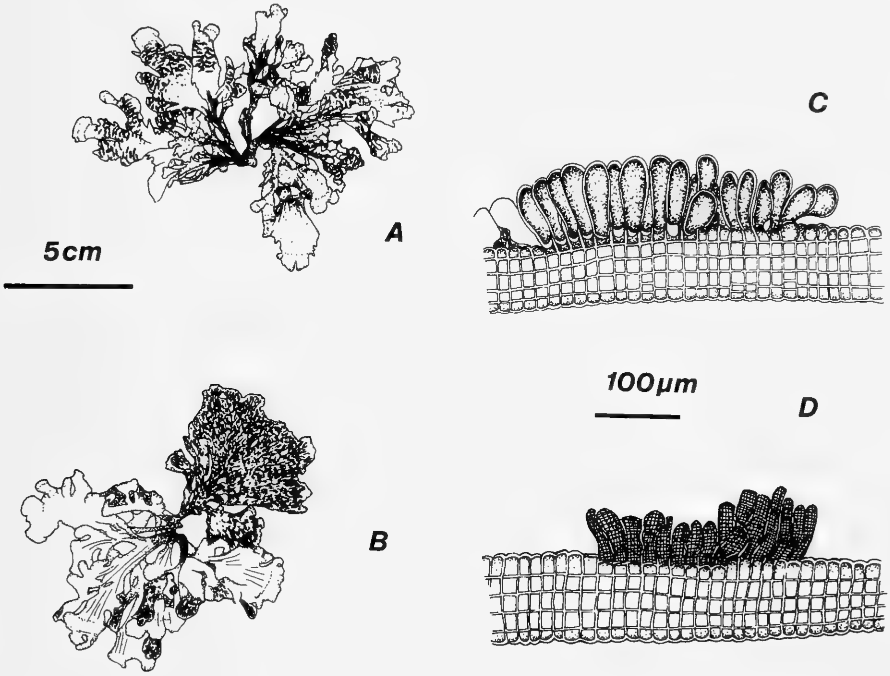


Fig. 21. Homoeostrichus olsenii: (**A**) habit of sporangial plant (UNSW 18242), (**B**) habit of male plant (UNSW 18243), (**C**) section of sporangial plant (UNSW 18216), (**D**) section of male plant (UNSW 18243).

Homoeostrichus olsenii Womersley, 1987:243.

Thalli 9-12cm long, a greyish colour; fronds 1-3(-6)cm wide (Fig. 21**A**,**B**), complanate, flabellate or irregular, with dense hairs covering most of the under surface; 5(-6) cells thick (Fig. 21**C**,**D**); sporangial sori (Fig. 21**C**) scattered across the frond in roughly concentric rows; male gametangia in orange-brown sori without paraphyses (Fig. 21**D**).

Seasonality: sporangial plants collected in April, July, September, October, and November; male plants in April and July.

Australian distribution: south-eastern Australia, Nora Creina, South Australia, to Sydney Harbour (Womersley, 1987); in the present study from three relatively rough water localities in the Sydney region, to depths of 21m.

Selected specimens examined: New South Wales: Fairlight, 2-3m, 16-ix-1985, *Farrant*, UNSW 18293; Fairlight, 2-3m, 8-vii-1985, *Farrant*, UNSW 18216; Dobroyd, 8-iv-1979, *Farrant*, UNSW 18779; Bare I., 6m, 25-vii-1985, *Farrant*, UNSW 18242 and UNSW 18243; Bare I., 10m, 17-x-1985, *Farrant*, UNSW 18567; Boat Harbour, 21m, 21-iv-1975, *Harada* R2361, NSW.

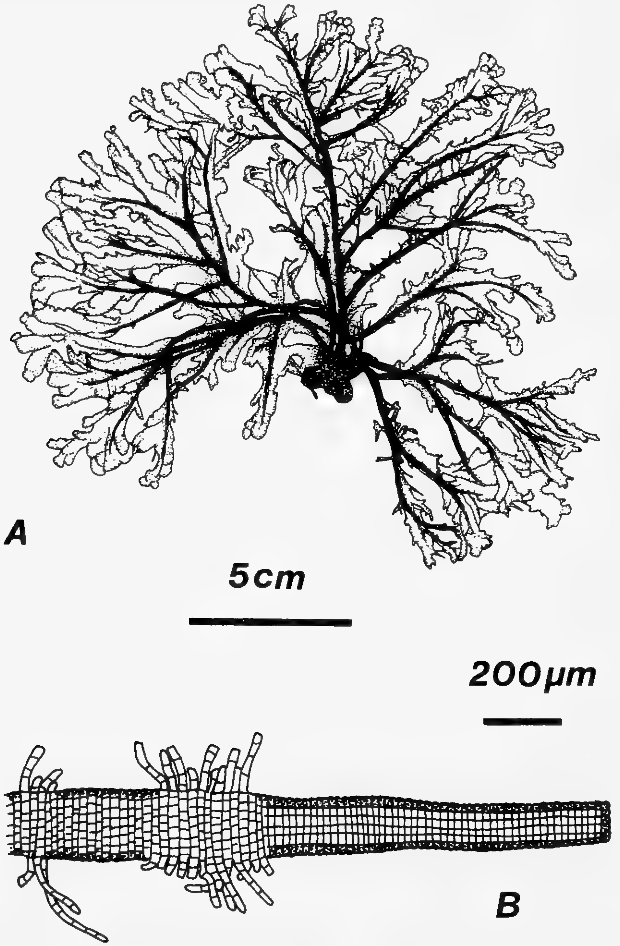


Fig. 22. Homoeostrichus sinclairii: (**A**) habit (UNSW 18020), (**B**) T.S. through frond 'midrib' (UNSW 18004).

Homoeostrichus sinclairii (Hooker and Harvey) J. Agardh, 1894:15; Womersley, 1987:242.

Zonaria sinclairii Hooker and Harvey, 1845:530.

Thalli 8-18cm long; fronds linear with cuneate terminal segments to about 1cm wide, narrowing below to a bare 'midrib' (Fig. 22**A**); hairs largely on 'midrib'; in transverse section generally 6 cells thick below the apex and expanded at the 'midrib' (Fig. 22**B**); sporangia with multicellular pedicels, amongst hairs.

Seasonality: collected throughout the year, with sporangial plants in all except the summer months; gametangial plants unknown for this species.

Australian distribution: southern and eastern Australia (Great Australian Bight to Newcastle) (Womersley, 1987), and as far north as Broughton Island, in relatively rough water localities and at depths greater than 2m.

Selected specimens examined: New South Wales: Broughton I., 2m, 28-iv-1985, *Farrant*, UNSW 18027; Norah Head, 19-iv-1978, *Kertesz*, UNSW 15308; Long Reef, 2-

vii-1975, *Harada* R4024, NSW; Dobroyd, 10m, 24-ix-1985, *Farrant*, UNSW 18535; Bare I., 5m, 6-iii-1986, *Farrant*, UNSW 18301; Plantation Point, 26-i-1974, *Larkum*, NSW.

COMPARISON WITH *HOMOEOSTRICHUS* SPECIES IN ADJACENT REGIONS

A third species, *Homoeostrichus canaliculatus* (J. Agardh) J. Agardh, is found in southern Australia but not in New South Wales. This species has linear fronds mostly 1-1.5mm wide and 6-7 cells thick (Womersley, 1987).

Stypopodium Kuetzing

Growth from a marginal row of apical cells. **Thalli** prostrate or erect, membranous; fronds in transverse section having cortical cells smaller than medullary cells and medullary cells not strictly tiered in transverse section; no sterile paraphyses associated with sporangia.

Stypopodium can easily be confused with *Taonia*. It differs from *Taonia* in having thick distal fronds, the fronds becoming 4 cells thick close to the apex (*Taonia* has thin distal fronds and becomes 4 cells thick at a distance from the apex, Fig. 23**A**); in *Stypopodium* there is an abrupt change in the size of cells from the cortex to the medulla with pigmented cortical cells much smaller (in *Taonia* there is no such abrupt change in cell size, Fig. 23**B**). Allender and Kraft (1983) also refer to the smoothly arching laciniae in most clumps of *Taonia* which are not seen in *S. australasica* (Zanardini) Allender and Kraft.

Stypopodium flabelliforme is the only species of the genus from the mainland New South Wales coast, although specimens exhibit some gradation towards both *S. australasicum* and *S. flabelliforme* var. *rabdoides* Allender and Kraft, both recorded for Lord Howe Island by Allender and Kraft (1983). Mainland New South Wales specimens are variable in habit (erect with single holdfast to decumbent with overlapping blades), frond shape (flabellate to lobed), and colour (light brown, iridescent, or with slightly darker longitudinal bands).

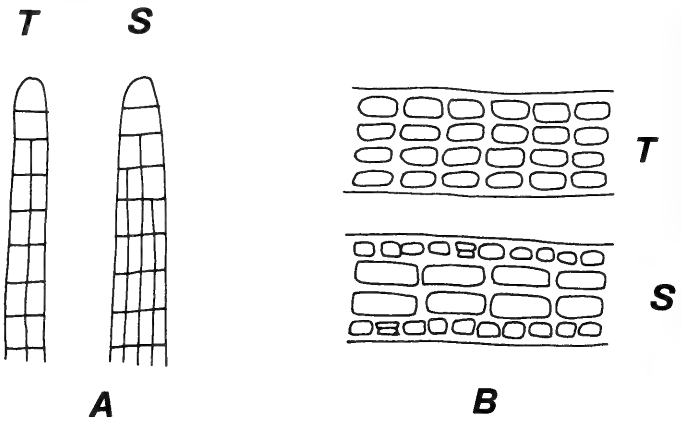
Stypopodium flabelliforme Weber-van Bosse, 1913:176. Allender and Kraft, 1983: 96.

Thalli 4-8cm long, usually decumbent although larger plants erect, brown, often iridescent (blue-green) with dark longitudinal bands not obvious on the brown dried thalli; fronds 2-9cm wide, flabellate and sometimes divided into irregular lobes (Fig. 24**A**,**B**); regular concentric hair lines sometimes present, especially on larger flabellate plants (Fig. 24**A**); fronds in section having a medulla 4-6 cells thick in the lower parts (Fig. 24**C**,**D**); sporangia densely scattered all over the fronds (except for conspicuous sterile bands next to the hair lines), or in patches.

Seasonality: collected in most months, sporangial plants in February, April and October; no gametangial plants.

Australian distribution: Lord Howe Island and the southern Great Barrier Reef (Allender and Kraft, 1983); Allender and Kraft (1983) were the first to record the species for the Australian mainland coast (Coffs Harbour, New South Wales, and Heron I., Queensland); in this study collected south to Jervis Bay, from the upper sublittoral to depths of 20m, mostly on open coasts.

Selected specimens examined: New South Wales: NW Solitary I., 10-16m, 6-x-1985, *Farrant*, UNSW 18603; Seal Rocks, 0-2m, 10-x-1985, *P. and W. Farrant*, UNSW 18679; Clovelly, 1-3m, 16-iv-1985, *Farrant*, UNSW 17781; Jervis Bay, 15m, 14-iv-1984, *Farrant*, UNSW 16201; Plantation Point, 30-vii-1973, *V. May*, NSW; Malau Bay, 21-viii-1987, *D. May*, MUCV 2570.



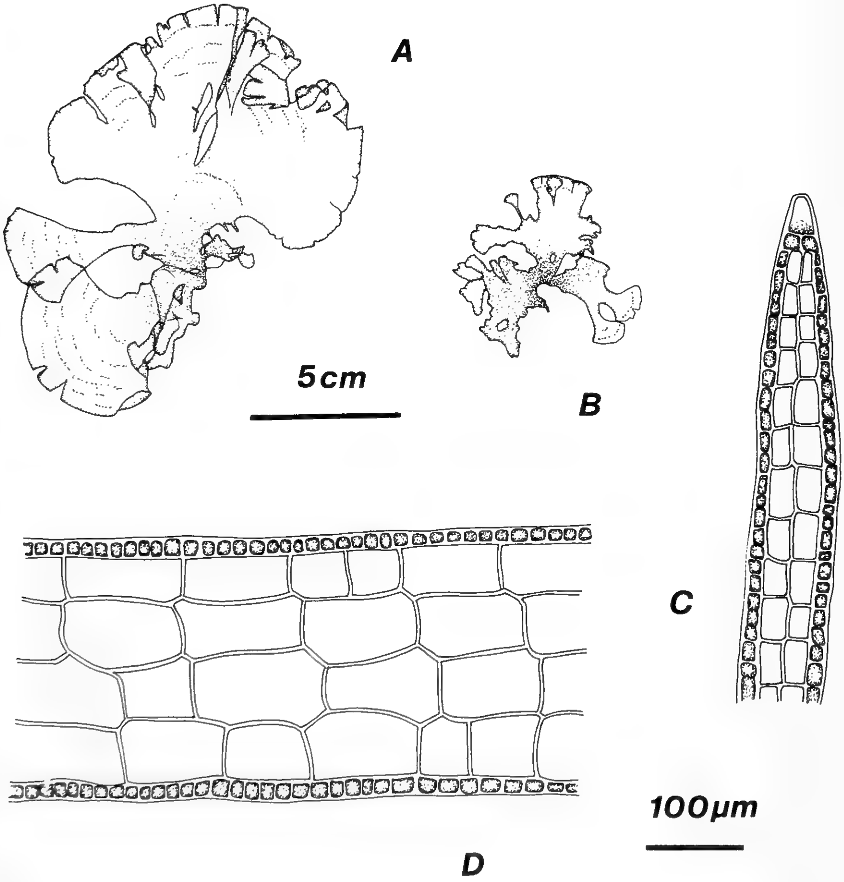


Fig. 23 (above). Diagrams showing the differences between *Taonia* (T) and *Stypopodium* (S): (**A**) L.S. apex, (**B**) T.S. lower part of frond.

Fig. 24 (below). *Stypopodium flabelliforme:* (**A**) habit of broad flabellate plant (UNSW 18601), (**B**) habit of smaller more prostrate plant (UNSW 17770), (**C**) L.S. through apex (UNSW 18043), (**D**) L.S. through frond (UNSW 18014).

COMPARISON WITH *STYPOPODIUM* SPECIES IN ADJACENT REGIONS

Two other taxa of *Stypopodium* are found at Lord Howe Island, *S. flabelliforme* var. *rabdoides* and *S. australasicum* (Allender and Kraft, 1983), and a further two have been recorded for northern Australia, *S. zonale* (Lamouroux) Papenfuss and *S. lobatum* Kuetzing (Lewis, 1985). The genus is not recorded in southern Australia.

Taonia J. Agardh

Growth from a marginal row of apical cells. **Thalli** erect, membranous; fronds flabellate, often deeply dissected; surface cells similar in size to medullary cells, distal part of frond thin, two cells thick, thicker in lower parts; sori scattered on frond in more or less concentric zones.

Taonia can be easily confused with *Stypopodium* (Fig. 23**A**,**B**) (see notes under that species). There is only one species of *Taonia* in New South Wales, *T. australasica*.

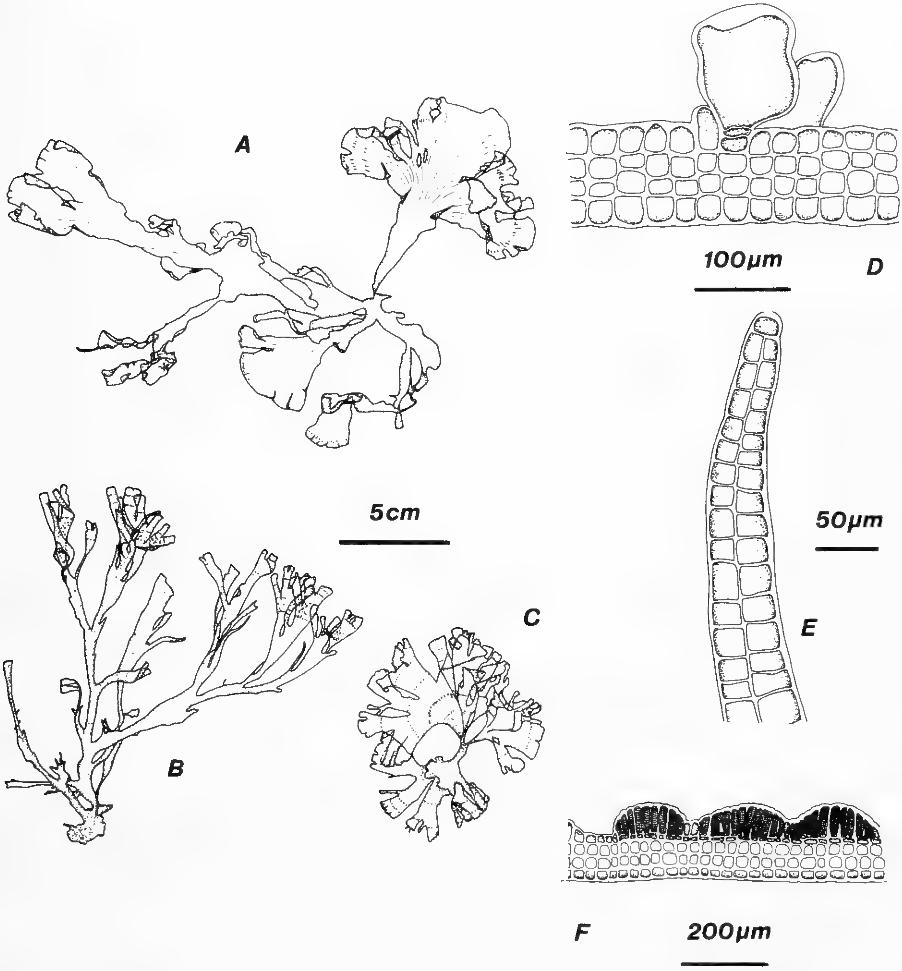


Fig. 25. Taonia australasica: (**A**) habit of large, broad plant (UNSW 18070), (**B**) habit of narrow fronded plant (UNSW 17634), (**C**) habit of broad plant (UNSW 17774), (**D**) T.S. through sporangium (UNSW 17634), (**E**) L.S. through apex (UNSW 18066), (**F**) T.S. through male gametangial sorus (UNSW 18234).

Taonia australasica J. Agardh, 1894:30. Allender and Kraft, 1983:91; Womersley, 1987:238.

Thalli 4-19cm long, tan-olive in colour at the top, dark brown at the base; fronds 0.5-17cm wide, flabellate (Fig. 25**A-C**), in transverse section cells similar in size throughout (Fig. 25**D**), thin, remaining 2 cells thick for some distance below the apex (Fig. 25**E**); sporangia borne on two stalk cells at maturity, sessile or partially embedded in the thallus (Fig. 25**D**); antheridia in indusiate sori on male plants (Fig. 25**F**).

Seasonality: collected in all months except December, but seasonally abundant with marked decrease in abundance and biomass in summer (King and Farrant, 1987); sporangial plants collected in all months of the year except October and December; the single male gametangial plant collected in July the first record of sexual reproduction for this species.

Australian distribution: south-eastern Australia, from Kangaroo Island, South Australia, to Coffs Harbour, New South Wales (Womersley, 1987), and Lord Howe Island (Allender and Kraft, 1983); found in the sublittoral below 2m depth at both open coast and estuarine localities (Sydney Harbour).

Selected specimens examined: New South Wales: Broughton I., 2m, 28-iv-1985, *Farrant*, UNSW 18024; Harbord, 1-2m, 16-ii-1985, *Farrant*, UNSW 17610; Fairlight, 1-2m, 16-iv-1986, *Farrant*, UNSW 18358; Mrs Macquarie's Point, 2m, 27-vi-1985, *Farrant and Puttock*, UNSW 18211.

COMPARISON WITH *TAONIA* SPECIES IN ADJACENT REGIONS

Taonia australasica is the only species of *Taonia* found in Australia. It is found in the regions adjacent to New South Wales, at Lord Howe Island, in Queensland and in southern Australia.

CONCLUSIONS

The algae of the New South Wales coastline have been much less studied than those on adjacent shores, especially those to the south. The Dictyotales are well represented in the flora with 22 species in 13 genera, and since they are abundant during most seasons especially in the upper sublittoral (King and Farrant, 1987) they are frequently referred to in ecological accounts. The present treatment has clarified the species encounted in New South Wales and provides keys and descriptions for their ready identification.

ACKNOWLEDGEMENTS

We would like to thank E. O'Brien, W. Farrant, and C. F. Puttock, for valuable assistance with field work; Dr B. M. Allender, Dr G. Kraft, D. May, Dr A. J. K. Millar, Dr J. Phillips, Mrs D. Sinkora, and Prof. H. B. S. Womersley for loan of specimens and for helpful discussion during the study; and MEL, MUCV and MELU herbaria for loan of specimens.

References

AGARDH, J. G., 1841. — In historiam algarum symbolae. *Linnaea* 15: 1-50.

——, 1848., — *Species, Genera et Ordines Algarum*. Vol. 1. Lund: Gleerup.

——, 1872. — Till algernes systematik. *Acta Univ. Lund.* 9: 1-71.

——, 1882. — Till algernes systematik. *Acta Univ. Lund.* 17: 1-136, pls 1-3.

——, 1894. — Analecta Algologica. Cont. I. *Acta Univ. Lund.* 29: 1-144, pl. 1.

ALLENDER, B. M., 1980. — *Dictyotopsis propagulifera* (Phaeophyta) — an algal enigma. *Phycologia* 19: 234-236.

——, and KRAFT, G. T., 1983. — The marine algae of Lord Howe Island (New South Wales): the Dictyotales and Cutleriales (Phaeophyta). *Brunonia* 6: 73-130.

ARESCHOUG, J. E., 1854. — Phyceae novae et minus cognitae in maribus extraeuropaeis collectae. *Acta Reg. Soc. Sci. Upsala, Ser III* 1: 329-372.

BOERGESEN, F., 1935. — A list of marine algae from Bombay. *K. Dan. Vidensk. Selsk. Biol. Meddr* 12: 1-64, pls. 1-10.

BOLD, H. C., and WYNNE, M. J., 1985. — *Introduction to the Algae. Structure and Reproduction.* 2nd Edition. Englewood Cliff, New Jersey: Prentice-Hall Inc.

BOROWITKZA, M. A., KING, R. J., and LARKUM, A. W. D., 1982. — Field guide to the marine plants of New South Wales. Chlorophyta, Phaeophyta, and Seagrasses. (Privately publ., Sydney). 70 pp.

BORY DE SAINT-VINCENT, J. B., 1827. — Padine. *Dict. Class. Hist. Nat.* 12: 589-91. Paris.

CRIBB, A. B., 1954. — Records of marine algae from south-eastern Queensland, I. *Pap. Dep. Bot. Univ. Qd* 3: 15-37.

EARLE, S. A., 1969. — Phaeophyta of the eastern Gulf of Mexico. *Phycologia* 7: 71-254.

EDELSTEIN, T., and WOMERSLEY, H. B. S., 1975. — The thallus and spore development of *Lobospira bicuspidata* Areschoug (Dictyotales): Phaeophyta. *Trans Roy. Soc. S. Aust.* 99: 149-156.

GEPP, A., and GEPP, E. S., 1906. — Some marine algae from New South Wales. *J. Bot.* 44: 249-261.

GREVILLE, R. K., 1830. — *Algae Britannicae.* Edinburgh: MacLachlan & Stewart.

HARVEY, W. H., 1860. — *Phycologia Australica.* Vol. III., London: Reeve.

HAUCK, F., 1887. — Über einige von J. M. Hildebrandt in Rothen Meere und Indischen Ocean gesammelte Algen. *Hedwigia* 2: 41-45.

HAUPT, A. W., 1932. — Structure and development of *Zonaria farlowii. Am. J. Bot.* 19: 239-254, pls XIX-XXII.

HOOKER, J. D., and HARVEY, W. H., 1845. — Algae Novae Zelandiae. *Lond. J. Bot.* 4: 521-551.

KING, R. J., and FARRANT, P. A., 1987. — The phenology of the Dictyotales (Phaeophyceae) at a sheltered locality in Sydney Harbour, New South Wales, Australia. *Bot. Marina* 30: 341-350.

LAMOUROUX, J. V. F., 1809. — Observations sur la Physiologie des Algues marines, et description de cinq nouveaux genres de cette famille. *Nouv. Bull. Sci. Soc. Philom. Paris* 1: 330-333, pl. 6.

LEVRING, T., 1940. — Die Phaeophyceengattungen *Chlanodiphora*, *Distromium*, und *Syringoderma. K. fysiogr. sallsk. Lund. Forh.* 10: 1-11.

LEWIS, J. A., 1985. — Checklist and bibliography of benthic marine macroalgae recorded from northern Australia. II. Phaeophyta. Department of Defence Materials Research Laboratories, Victoria. Report MRL-R-962, 40 pp.

LINDAUER, V. W., CHAPMAN, V. J., and AIKEN, M., 1961. — The marine algae of New Zealand. II: Phaeophyceae. *Nova Hedwigia* 3: 129-350.

LUCAS, A. H. S., 1909. — Revised list of the Fucoideae and Florideae of Australia. *Proc. Linn. Soc. N.S.W.* 34: 9-61.

——, 1913. — Notes on Australian marine algae. i. Fucoideae. *Proc. Linn. Soc. N.S.W.* 38: 49-60.

——, 1914. — Marine algae. *British Association for the Advancement of Science. Handbook for N.S.W.*: 459-463. Sydney: Edward Lee & Co.

——, 1935. — The marine algae of Lord Howe Island. *Proc. Linn. Soc. N.S.W.* 60: 194-232.

MAY, V., 1939. — A key to the marine algae of New South Wales — Part II. Melanophyceae (Phaeophyceae). *Proc. Linn. Soc. N.S.W.* 64: 191-215.

——, BENNETT, I., and THOMPSON, T. E., 1970. — Herbivore-algae relationships on a coastal rock platform (Cape Banks, N.S.W.). *Oecologia (Berl.)* 6: 1-14.

——, COLLINS, A. J., and COLLETT, L. C., 1978. — A comparative study of epiphytic algal communities on two common genera of sea-grasses in eastern Australia. *Aust. J. Ecol.* 3: 91-104.

——, and LARKUM, A. W. D., 1981. — A subtidal transect in Jervis Bay, New South Wales. *Aust. J. Ecol.* 6: 439-457.

NGAN, Y., and PRICE, I. R., 1979. — The intertidal algae of the mainland coast in the vicinity of Townsville, Queensland, tropical Australia. *Atoll Res. Bull.* 237: 1-29.

——, and ——, 1980. — Seasonal growth and reproduction of intertidal algae in the Townsville region (Queensland, Australia). *Aq. Bot.* 9: 117-134.

PAPENFUSS, G. F., 1943. — Notes on algal nomenclature. II. *Gymnosorus* J. Agardh. *Am. J. Bot.* 30: 463-468.

——, 1944. — Notes on algal nomenclature. III. Miscellaneous species of Chlorophyceae, Phaeophyceae and Rhodophyceae. *Farlowia* 1: 337-346.

——, 1952. — Notes on South African marine algae. III. *J. S. Afr. Bot.* 17: 167-188.

READER'S DIGEST, 1977. — *Atlas of Australia.* Sydney: Reader's Digest Services Pty Ltd.

SONDER, W., 1871. — Die Algen des tropischen Australiens. *Abh. naturw. Ver. Hamburg* 5: 33-74, plates 1-6.

SONDER, O. G., 1880. — I. Algae Australianae hactenus cognitae. In: *Fragmenta phytographiae Australiae*, Suppl. ad. Vol. II (F. Mueller): 1-42. Melbourne.

WEBER-VAN BOSSE, A., 1913. — Liste des algues du Siboga. I. Myxophyceae, Chlorophyceae, Phaeophyceae. *Siboga Exped. Monogr.* 59a: 1-186.

WOMERSLEY, H. B. S., 1949. — Studies on the marine algae of southern Australia. No. 3. Notes on *Dictyopteris* Lamouroux. *Trans Roy. Soc. S. Aust.* 73: 113-116.

——, 1967. — A critical survey of the marine algae of southern Australia. II. Phaeophyta. *Aust. J. Bot.* 15: 189-270.

——, 1981. — Biogeography of Australasian marine macroalgae. In: M. N. CLAYTON and R. J. KING, (eds), *Marine Botany: an Australasian Perspective*: 292-307. Melbourne: Longman Cheshire.

——, 1987. — *The Marine Benthic Flora of Southern Australia.* Part II. Adelaide: South Australian Government Printing Division.

——, and BAILEY, A., 1970. — Marine algae of the Solomon Islands. *Phil. Trans Roy. Soc. Lond.* B. *Biol. Sci.* 259: 257-352.

YAMADA, Y. 1931. — Notes on some Japanese algae. II. *J. Fac. Sci. Hokkaido Imp. Univ. Ser.* 5 1: 65-76.

A distinctive new Species and new Distribution Records of Stilbopteryginae (Insecta: Neuroptera: Myrmeleontidae)

C. N. SMITHERS

SMITHERS, C. N. A distinctive new species and new distribution records of Stilbopteryginae (Insecta: Neuroptera: Myrmeleontidae). *Proc. Linn. Soc. N.S.W.* 110 (4), (1988) 1989: 407-410.

Stilbopteryx mouldsorum sp. n., a very distinctive species of lacewing, is described from Western Australia. It has a colour pattern not found in any known species of the genus. New distribution records, based on material in the collections of the Australian and Queensland Museums are given for the other species of Stilbopteryginae.

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manuscript received 12 April 1988, accepted for publication 20 July 1988.

INTRODUCTION

The genus *Stilbopteryx* Newman, with six described species, and *Aeropteryx* Riek, with three species, constitute the subfamily Stilbopteryginae of the Myrmeleontidae. They include some of the largest and most spectacular Australian lacewings. Some species have a wing length of up to 50mm. Very little is known of the biology of this group. Of only one species (*S. linearis* Navas) is the larva known (McFarland, 1968). Development from egg to adult took six years in culture. Both sexes of the species of *Stilbopteryx* are known, except for *S. albosetosa* Riek of which males have not been found. All three species of *Aeropteryx* are known from males only.

Riek (1968) published a key which included six of the seven species known at the time. Later (Riek, 1976) he described two more species and included them, with all seven previously known, in a revised key. He also listed the synonyms for each and gave information on the distribution of the species. New (1982) discussed the status of the genera, which at that time were usually included in the family Stilbopterygidae. He gave reasons for considering them to constitute a subfamily of the Myrmeleontidae.

During study of collections in the Australian and Queensland Museums a female of a very distinctive, undescribed species of *Stilbopteryx* was found as well as material which increased knowledge of the distribution of the other species. This material forms the basis of this note. For the sake of completeness the previously known distributions of the species are summarized.

In the list of material the initials 'M.S.M.' and 'B.J.M.' indicate specimens collected by M. S. and B. J. Moulds respectively and 'AM' and 'QM' the Australian and Queensland Museums.

DESCRIPTION AND RECORDS

Stilbopteryx mouldsorum sp.n.

Female: Head very dark brown, slightly paler on each side of epicranial suture. Front of head anterior to lower level of eyes creamy yellow. Antennae very dark brown, club with pale transverse bands. Setae on scape black. Pronotum dark brown with creamy yellow bands along anterior and posterior margins. Setae black. Pterothorax dorsally dark brown. Setae on anterior half of mesonotum mostly black, some thoracic setae white. Thorax laterally grey-brown, setae mostly white. Legs very dark brown. Abdominal segment 1 very dark brown; segment 2 very dark brown with narrow creamy yellow posterior border; segments 3-6 very dark brown with very broad anterior and posterior creamy yellow bands; segment 7 similar but bands narrower. There is as much creamy yellow area as darker colour in the basal half of the abdomen. Ectoprocts very dark brown with creamy yellow postero-dorsal border and similarly coloured patch near base. Eighth and ninth tergites very dark brown with paler hind borders. Posterior gonapophyses long and narrow with black setae, similar to those of *S. linearis* Navas. Fore wings with costal area hyaline but dark brown just basad of creamy yellow pterostigma. Radial area with infuscation reaching hind margin of area distally before pterostigma. The dark brown band formed by these coloured areas is continued beyond the pterostigma adjacent to the wing margin anteriorly, around the wing apex and along hind margin of wing, tapering to end about half way along hind margin. Costal crossveins, Rs and its branches and veins and crossveins posterior to CuA creamy yellow. Other veins dark brown. Hind wing costal area brown almost from base with crossveins nearly all brown. Other markings as in fore wing but veins and crossveins posterior to CuA mostly brown. Fore wing length: 45mm. Body length: 42mm.

Male: Not known.

Material examined: 1 ♀ (holotype), Western Australia, 3km from West Strelley River, approx. 70km SE Port Hedland, 16.ii.1977. M.S. and B.J. Moulds. Holotype in Australian Museum.

Discussion: *Stilbopteryx mouldsorum* is recognizable by its colour pattern. It is the only species in the subfamily in which the brown band along the front of the wing is continued beyond the apex and along the hind margin. The creamy yellow pronotal marks are more extensive and stand out more clearly than in other species. The similarly coloured areas on the abdomen are so extensive and conspicuous that they give the abdomen a banded appearance. In other species these areas are much smaller and appear as isolated spots.

Stilbopteryx linearis Navas

Recorded distribution. *South Australia:* SE Lake Eyre North, near Muloorina homestead; Prescott Point, Madigan Gulf, Lake Eyre North; Killalpanima, 160km E Lake Eyre.

New record. *South Australia:* 1 ♀, Arkoola, northern Flinders Ranges, 21.i.1976, M.S.M. and B.J.M. (AM).

Stilbopteryx albosetosa Riek

Recorded distribution. *Northern Territory:* Murella Park; Daly Waters; Jabaluka Lagoon, 14km N. Mudginbarry head station; 1km S Cahill's Crossing, East Alligator R; 5km NNW Cahill's Crossing, East Alligator R.

New records. *Northern Territory:* 3 ♀, Waterhouse R., Mataranka Hstd., 23.xii.1968; 1 ♀, McArthur R., 15km S junction Carpentaria/Tablelands Highway, 12.1.1986, M.S.M. and B.J.M. (AM). *Queensland:* 1 ♀, Almaden, Chillagoe dist., i.1932, W. D. Campbell; 1 ♀, swamp, 28km N Leura, 30.xi.1974; 2 ♀, East Haydon, 60km SE Normanton, 15.i.1986, M.S.M. and B.J.M. (AM).

Stilbopteryx walkeri Kimmins

Recorded distribution. *Queensland:* Moreton Bay; Fletcher; Eidsvold; Rifle Range, Biggenden; Bundaberg; Crystal Creek, 35km SE Ingham; Clermont; Stradbroke Is.; Carnarvon Range; Almaden, Chillagoe dist.

New records. *Queensland:* 2 ♂, Moffat Nat. Park, The Chimneys, 14.xii.1987, Monteith, Thompson, Yeates; 1 ♀, Blackdown Tablelands, via Dingo, 1984, S Pearson (QM); 1 ♀, Miriam Vale, Mt Larcom area, 27.xii.1966; 1 ♀, Bauple, 14.xii.1977; 1 ♂, Doolandella, Brisbane, 12.i.1985; 1 ♂, Boomerang Range, 30km W Marlborough, 8.xii.1980; 1 ♀, Lawn Hill Creek, Adel's Grove, W Gregory Downs, 19.xii.1986, M.S.M. and B.J.M. (AM). *New South Wales:* 1 ♀, 20km N Grafton, 21.i.1975, J. Frazier; 1 ♂, Calumet, 26km NE Binnaway, 16.xii.1931, C. F. Garnsey; 1 ♀, Wheeogo, near Dunedoo, i.1971, W. Gaden; 1 ♀, Mann R., 5km upstream from Old Glen Innes—Grafton Rd., crossing, 16.xi.1977, M.S.M. and B.J.M. (AM).

Stilbopteryx napoleo (Lefebvre)

Recorded distribution. *Western Australia:* Waroona; Yallingup; Swan R.; Yanchep; Perth; 'NW New Holland'; 'South and west Autralia'. *Northern Territory:* 99km NNW Alice Springs. *South Australia:* Coorong Nat. Park.

New records. *Western Australia:* 1 ♀, 30km S Mendurah, 13.1.1971; 1 ♀, Waylunga Nat. Park, 35km NW Perth, 6.1.1971; 2 ♂, 1 ♀, John Forrest Nat. Park, Darling Ranges, 21-23.i.1971, G. A. Holloway and H. Hughes (AM).

Stilbopteryx costalis Newman

Recorded distribution. *New South Wales:* Sydney; Shoalhaven; 42km NE Binnaway. *Queensland:* Stradbroke Is.

New records. *Queensland:* 1 ♂, Brisbane, 4.xi.1936; 1 ♂, 1 ♀, Carnarvon Range, 7.xii.1941; 1 ♀, Milmerran, 21.xii.1941, J. Macqueen (QM); 1 ♀, Cloncurry, 19.i.1984, M.S.M. and B.J.M. (AM). *New South Wales:* 1 ♀, Waterfall, 31.xii.1978, D. Doolan; 1 ♂, Loftus, 27.xii.1978, J. Olive; 1 ♂, Engadine, 16. xii.1976, M. Schneider; 1 ♂, Como, 9.xi.1961, L. Willan; 1 ♀, Norton's Basin, Nepean R., 19.xii.1916, A. Musgrave (AM).

Stilbopteryx auricornis Kimmins

Recorded distribution. *Western Australia:* Sherlock R.; Pinjara; 32km WSW Mt Magnet; 30km SE by S Carnarvon.

New records. *Western Australia:* 1 ♀, Carnarvon, 25.ii.1977, M.S.M. and B.J.M. 1 ♀, Marble Bar, 18.i.1974, G. Jones (AM). *South Australia:* 1 ♂, 1 ♀, Stuart Highway, 56km S Northern Territory border, 4.ii.1986, M.S.M. and B.J.M. (AM). *Northern Territory:* 3 ♀, Yalora Resort, Ayer's Rock, 1.ii.1984, M.S.M. and B.J.M. (AM).

Aeropteryx brocki (Manski)

Recorded distribution. *Queensland:* Kalpower; Little Crystal Creek, Mt Spec; Bluff Range, Biggenden.

New records. *Queensland:* 1 ♂, Edungalba, near Duaringa, 24.i.1982, M.S.M. and B.J.M. (AM); 2 ♂, Blackdown Tableland, via Dingo, xii.1978, Maywald, Czechura (QM).

Aeropteryx gibba Riek

Recorded distribution. *Northern Territory:* Deaf Adder Creek; Murella Park; Katherine Gorge; 7km NW by N Cahill's Crossing, East Alligator R.; 9km N by E Mudginbarry head station.

New records. *Northern Territory:* 1 ♂, Barkly Highway, 75km ESE junction with Tablelands Highway, 4.i,1987. M.S.M. and B.J.M. (AM). *Queensland:* 3 ♂, Little R., E Croydon, 15.xii.1986; 1 ♂, Iron Range, xi.1985, G. Wood (QM). *Western Australia:* 2 ♂, Kununurra, 6-7.i.1986, M.S.M. and B.J.M. (AM).

Aeropteryx monstrosa Riek

Recorded distribution. *Queensland:* Station Creek Spring, Silver Plains, Cape York. Eidsvold. Hammond Is.

New record. *Queensland:* 1 ♂, Station Creek, 15km N Mt Molloy, 30.xii.1973, A. and M. Walford-Huggins (AM).

ACKNOWLEDGEMENTS

I would like to thank the many collectors of the material listed, especially Max and Barbara Moulds, for the considerable amount of material donated to the Australian Museum. The Director of the Queensland Museum kindly allowed me to study its material.

References

McFarland, N., 1968. — (Cover picture.) *Friends of S. Aust. Mus.* 7: 1-2.

New, T. R., 1982. — A reappraisal of the status of the Stilbopterygidae. (Neuroptera: Myrmeleontidae). *J. Aust. ent. Soc.* 21: 71-75.

Riek, E. F., 1968. — A new genus and key to species of Australian Stilbopterygidae (Neuroptera). *J. Aust. ent. Soc.* 7; 105-108.

———, 1976. — The family Stilbopterygidae (Neuroptera) in Australia. *J. Aust. ent. Soc.* 15: 297-302.

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VOLUME 110

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PROCEEDINGS of LINNEAN SOCIETY OF NEW SOUTH WALES
VOLUME 110

Issued 13th January, 1989

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NUMBER 4

Printed by Southwood Press Pty Limited,
80-92 Chapel Street, Marrickville 2204