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INFAUNA OF MARINE SEDIMENTS AND SEAGRASS BEDS OF UPPER SPENCER GULF NEAR PORT PIRIE, SOUTH AUSTRALIA

BY P. A. HUTCHINGS, T. J. WARD**, J. H. WATERHOUSE** & L. WALKER****

Summary

The infauna of six intertidal and shallow subtidal habitats were sampled in summer and winter near Port Pirie, Upper Spencer Gulf. The habitats included seagrasses and non-vegetated sediments. Over 12,000 individuals belonging to 372 taxa were collected in the survey. The species composition of this fauna had very little overlap (only 24 species) with that of a more recent survey of Northern Spencer Gulf. The density of the fauna in our study area was least (280 m^{-2}) in the unvegetated intertidal habitat, and highest (2612 m^{-2}) in the intertidal seagrass habitat *(Zostera),* and was dominated by polychaetes, molluscs and crustaceans. The fauna of the *Zostera* and *Posidonia* habitats is compared with other similar habitats sampled in southern Australia, in terms of the number of species, density of individuals and feeding guilds of the fauna. Differences in species diversity and densities between this study and other studies are likely to reflect the intensity of sampling, as well as differences between locations in the density and species of seagrass and in the prevailing hydrological regimes.

KEY WORDS: *Posidonia, Zostera,* seagrass beds, unvegetated sediments, infauna.

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The infauna of six intertidal and shallow subtidal habitats were sampled in summer and winter near Port Pirie, Upper Spencer Gulf. The habitats included seagrasses and non-vegetated sediments. Over 12,000 individuals belonging to 372 taxa were collected in the survey. The species composition of this fauna had very little overlap (only 24 species) with that of a more recent survey of Northern Spencer Gulf. The density of the fauna in our study area was least (280 m^{-2}) in the unvegetated intertidal habitat, and highest (2612 m^{-2}) in the intertidal seagrass habitat (*Zostera*), and was dominated by polychaetes, molluscs and crustaceans. The fauna of the *Zostera* and *Posidonia* habitats is compared with other similar habitats sampled in southern Australia, in terms of the number of species, density of individuals and feeding guilds of the fauna. Differences in species diversity and densities between this study and other studies are likely to reflect the intensity of sampling, as well as differences between locations in the density and species of seagrass and in the prevailing hydrological regimes.

KEY WORDS: *Posidonia*, *Zostera*, seagrass beds, unvegetated sediments, infauna.

Introduction

Upper Spencer Gulf near Port Pirie (33°19'S, 138°E), South Australia, is shallow (generally less than 20 m deep) and fringed with large expanses of intertidal mudflats, intertidal seagrasses (*Zostera* spp.), and subtidal beds of the seagrasses *Posidonia australis* and *P. sinuosa*. These shallow expanses of seabed are fished commercially and recreationally for a number of species of fish, including garfish and whiting, and for crustaceans including prawns and crabs (Jones 1979[1]; King 1977[2]). Although these, and many other species, use the seagrass beds and intertidal flats at various stages of their life cycle (Jones 1979[1]), there have been few ecological studies designed to document other species of importance occurring in these habitats of the Gulf.

Upper Spencer Gulf refers to the area of the Gulf between Port Davis Creek (just south of Port Pirie) and Ward Spit, and Northern Spencer Gulf is defined as the portion of Spencer Gulf north of Ward Spit, i.e. north of 33°S (Stefanson 1977). Spencer Gulf, is hypersaline, with salinities gradually increasing from 35 ‰ to more than 60 ‰ near Port Augusta at the head of the Gulf (Bullock 1975). Upper Spencer Gulf has an intermediate salinity regime, varying annually from about 41-47.2 ‰ and water temperatures ranging from 10-26.2°C (Dow 1980[3]). Studies of fish and crustaceans in this area by Ward & Young (1982) have shown that they appear to be unaffected by the constant high salinities.

In this study we examine the mainly invertebrate fauna living in the sediments in shallow-water habitats found in Upper Spencer Gulf near Port Pirie, and its species composition. These results are compared with those obtained from similar habitats elsewhere in southern Australia.

Similar habitats which have been studied in detail elsewhere in southern Australia are those of seagrass beds and intertidal habitats. The infauna of seagrass beds has been examined in several studies in eastern Australia (Collett *et al.* 1984; Hutchings & Recher 1974), and in Western Australia (Hutchings *et al.* 1991; Wells *et al.* 1985) and reviewed by Howard *et al.* (1989). The infauna of intertidal habitats in Northern Spencer Gulf has recently been studied by Ainslie *et al.* (1989).

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*** formerly of The Australian Museum now of 306, Molesworth St., Lismore, NSW 2480

[1]JONES, G. I. (1979) Biological Investigations of the Marine Scale Fishery in Spencer Gulf. (Dept Agriculture and Fisheries, South Australia). 72pp.

[2]KING, M. G. (1977) The biology of the Western King Prawn *Penaeus latisulcatus* Kishinouye and aspects of the fishery in South Australia. MSc. thesis, University of Adelaide, unpubl.

[3]DOW (1980) Redcliff Project – Draft Environmental Effects Statement. 178 pp. (Dow Chemical (Australia) Limited, Adelaide S.A.).

Materials and Methods

Samples of sediment were collected at high tide from 18 sites representing six habitats, by divers using PVC corers (220 mm diameter and 160 mm depth) in winter (25.vii.1979 – 17.xiii.1979) and in summer (1.ii.1980 – 1.iii.1980). Each corer had a sharpened leading edge and was capped at the other end by a PVC plate welded in place. A 50 mm hole in the cap covered with 1 mm fibreglass mesh allowed water to escape as the corer was driven into the sediment, and, after coring, was sealed with a rubber bung. No attempt was made to avoid seagrass leaves when they occurred at a sampling site, and the sampling technique resulted in substantial amounts of live and dead seagrass leaf material, rhizomes and roots in the samples. The habitats sampled (Fig. 1) were from about mid-tidal level (on mudflats adjacent to the mangroves) to sediments in 10 m water depth, and are the same habitats in which detailed studies of sediments and epibenthic fauna have been carried out previously (Ward & Young 1981, 1982). The habitats included bare intertidal muds (Sites 1A, 1B, 1C), intertidal seagrass beds of *Zostera mucronata* (Sites 2A, 2B, 2C), subtidal beds of *Posidonia australis* (Sites 3A, 3B, 3C) and *Posidonia sinuosa* (Sites 4A, 4B, 4C) and bare unvegetated

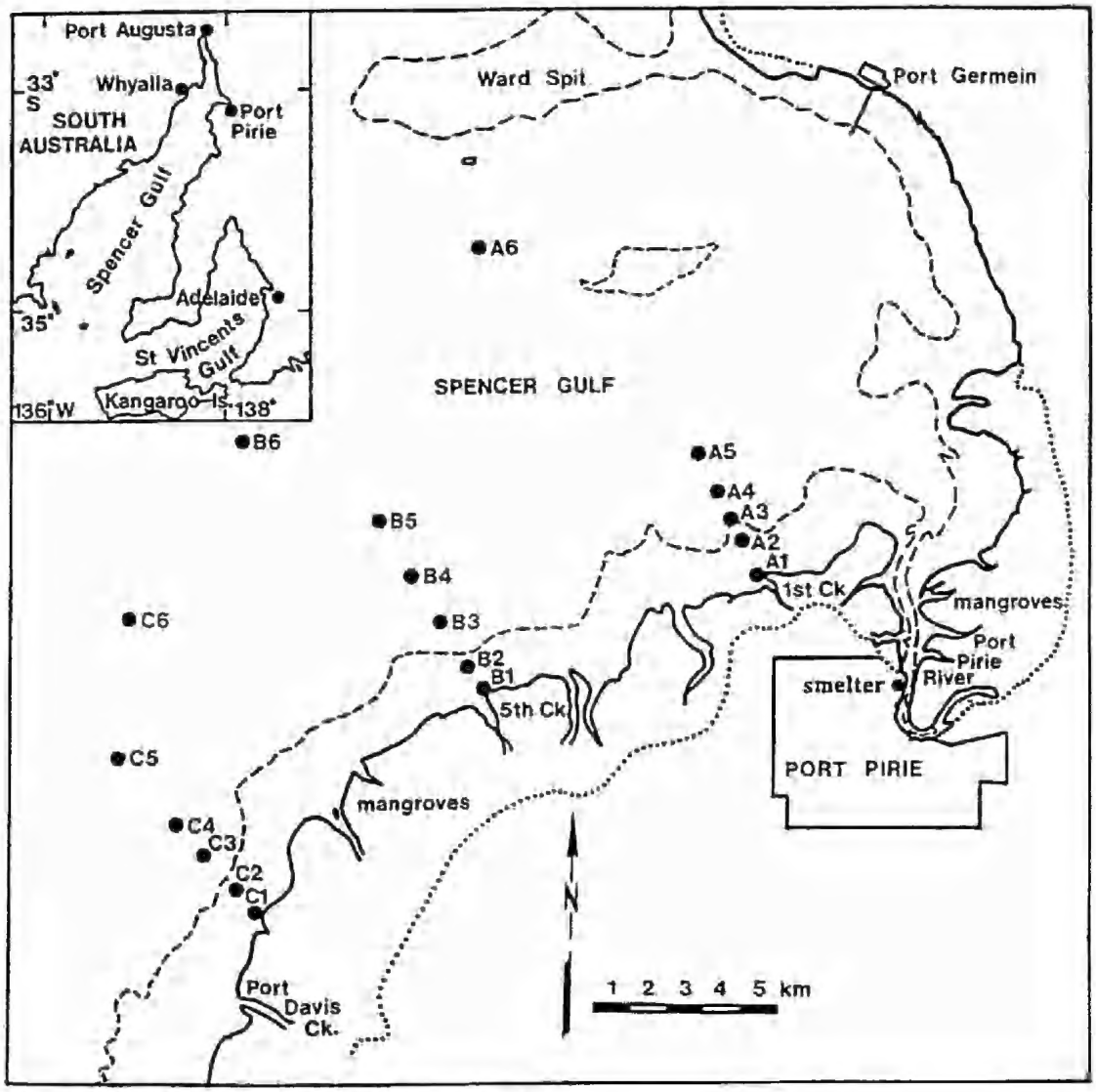

Fig. 1. The Port Pirie study area in Upper Spencer Gulf.

sediments (Sites 5A, 5B, 5C and Sites 6A, 6B, 6C) in deeper water (Fig. 1). At each site three samples were collected haphazardly from each of three plots of about 4 m^2 separated by at least 5 m. This resulted in nine samples from each of the 18 sites, collected in winter and summer, except for summer, when one sample from the *Posidonia australis* habitat was lost.

The samples were sieved in the field through 2 mm mesh and all residues were preserved in 10% formalin. In the laboratory the samples were sorted under water in large flat trays with the aid of low-power magnification. Hermit crabs were discarded because of the difficulty of extracting them from their shells, but all other non-colonial fauna was collected. Colonial organisms such as bryozoans and hydroids attached to the blades of the seagrasses were not sampled in this study. Because of taxonomic difficulties and a lack of funds the collection was stored for six years until resources permitted a detailed evaluation. The collection has been deposited at the Australian Museum, Sydney.

Results and Discussion

Species Composition of the Fauna

The samples contained 12,396 individuals representing 372 taxa. These taxa consisted of 39% polychaetes, 26% molluscs, 22% crustaceans, and 6% echinoderms, with the remaining 7% being distributed among the minor phyla (Table 1). The distribution and abundance of all taxa within the six habitats sampled is shown in Appendix 1. Of the 26 dominant taxa, defined as those represented by 100 or more individuals in the collection, 18 were polychaetes, four were molluscs, three were crustaceans and one was a holothurian (Table 2). The taxa identified as nemerteans and sipunculans may not be monospecific because of difficulties in identifying individuals to the species level. The most abundant species was *Tanais dulongi*, a tanaid crustacean.

The six habitats sampled varied considerably in the number of species present. The four subtidal habitats all had a high numbers of species (173 – 193) compared to the intertidal *Zostera* habitat (116), and

TABLE 1. *Infauna of Upper Spencer Gulf.* Numbers of species (S), density (d, number of individuals m^{-2}), abundance (n, % of total individuals in habitat) and total abundance (N) of the major taxa in each of the six habitat types sampled. All habitats were sampled with 54 cores (total surface area of 2.05 m^{-2}), except *Posidonia australis* which was sampled with 53 (total surface area of 2.01 m^{-2}).

taxa	habitat						
	intertidal	*Zostera*	*P. australis*	*P. sinuosa*	5m bare	10m bare	total
polychaetes							
S	12	57	94	97	91	88	148
d	243	1262	884	630	501	242	626
n(%)	87	48	76	73	76	49	62
crustaceans							
S	5	20	34	44	23	18	81
d	16	907	120	76	28	19	19
n(%)	6	35	10	9	4	4	19
molluscs							
S	6	23	34	32	38	50	95
d	13	330	84	95	92	183	133
n(%)	5	13	7	11	14	37	13
ascidians							
S	0	4	3	5	7	2	10
d	-	11	6	11	16	11	9
n(%)	-	0.5	0.5	1	2	2	1
echinoderms							
S	1	3	10	12	9	10	20
d	0.5	39	37	38	14	32	27
n(%)	0.2	2	3	4	2	7	3
minor taxa*							
S	2	8	6	4	3	4	18
d	8	62	27	11	9	10	21
n(%)	3	2	2	1	1	2	2
all taxa							
S	26	115	181	194	171	172	372
N	574	5362	2329	1764	1350	1017	12396
d	280	2612	1157	860	660	497	1010

* Minor taxa includes fish, insects, sipunculans, poriferans, nemerteans, pycnogonids, enteropneusts and hirudineans.

TABLE 2. *Abundances (%) of the dominant species — total abundances of 100 or greater — in each of the the six habitat types.*

	intertidal	*Zostera*	*P. australis*	*P. sinuosa*	5m bare	10m bare	total
Tanais dulongii	26 (3)	819 (97)	-	-	-	1 (0.1)	846
Capitella "capitata"	51 (8)	611 (92)	-	-	-	-	662
Nereis bifida	-	31 (5)	577 (89)	29 (5)	7 (1)	1 (0.2)	645
Apseudes australis	-	513 (87)	63 (11)	2 (0.3)	7 (1)	3 (0.5)	588
Leitoscoloplos sp.	31 (5)	414 (71)	121 (21)	13 (2)	1 (0.2)	-	580
Nephtys gravieri	109 (20)	99 (18)	13 (2)	115 (21)	149 (27)	67 (12)	552
Ceratonereis sp. 1	248 (65)	8 (2)	34 (9)	14 (4)	69 (18)	10 (3)	383
Pista violacea	-	340 (91)	6 (2)	12 (3)	3 (0.8)	12 (3)	373
Platynympha longicaudata	2 (0.6)	291 (90)	22 (7)	8 (2)	-	-	323
Barantolla sp.	-	88 (31)	57 (20)	88 (31)	46 (16)	6 (2)	285
Austromytilus penectus	-	5 (2)	2 (0.8)	2 (0.8)	57 (21)	211 (76)	277
Nematonereis unicornis	-	-	103 (41)	118 (47)	25 (10)	7 (3)	253
Augeneria verdis	-	131 (55)	18 (8)	49 (20)	26 (11)	16 (7)	240
Tellina deltoidalis	-	226 (95)	-	8 (3)	5 (2)	-	239
Zeacumantis diemenensis	1 (0.5)	206 (99)	-	-	-	-	207
Eunice sp. 3	-	-	41 (21)	72 (36)	51 (26)	35(18)	199
Notomastus sp. 1		2 (1)	96 (52)	51 (27)	25 (13)	12 (6)	186
Tellina mariae	6 (3)	71 (41)	20 (12)	45 (26)	12 (7)	18 (10)	172
Leptosynapta dolabrifera	-	74 (49)	42 (28)	33 (22)	-	1 (0.7)	150
Asychis sp.	-	-	5 (4)	2 (1)	115 (82)	19 (13)	141
Cirriformia sp. 1	-	43 (34)	43 (34)	28 (22)	4 (3)	9 (7)	127
Caulleriella sp. 4	-	20 (18)	31 (27)	38 (34)	21 (19)	3 (3)	113
Eunice sp. 1	-	-	5 (5)	81 (74)	19 (17)	4 (4)	109
Diplocirrus sp.	-	92 (90)	3 (3)	4 (4)	1 (1)	2 (2)	102
Scoloplos simplex	1 (1)	74 (73)	17 (17)	4 (4)	4 (4)	1 (1)	101
Caulleriella sp. 3	-	7 (7)	35 (35)	43 (43)	14 (14)	1 (1)	100
totals	475 (6)	4165 (52)	1354 (17)	859 (11)	661 (8)	439 (6)	7953
total abundance (all species)	574	5362	2329	1764	1350	1017	12396
% abundance dominant/abundance total	83	78	58	49	49	43	64

the intertidal mud, which was by far the most species-poor habitat with only 27 species recorded (Table 1). The pattern of densities amongst the six habitats was generally similar to that of species richness except for the *Zostera* habitat. This habitat had the highest density of fauna (2612 individuals m^{-2}) with the second lowest species richness (115 spp.).

Overall, polychaetes and molluscs were the two dominant groups in terms of both numbers of species and individuals. The crustaceans were generally similar to the molluscs in species richness and abundance in the two *Posidonia* habitats and the intertidal mud, but were considerably reduced in the two subtidal unvegetated habitats. Echinoderms, ascidians and the

minor taxa were represented by only few species and typically few individuals in all habitats.

Of the 12,396 individuals collected 7,953 (64%) belonged to only 26 (7%) of the 375 species. The remaining 346 species were represented in most cases by only a few individuals (Appendix 1). Ninety-four species were represented by only a single individual in the collection and 155 species were present in only one habitat. Similar patterns have been found in other studies of the infauna of Australian seagrass beds (Collett *et al.* 1984; Hutchings *et al.* 1991).

The 26 dominant species were distributed unevenly between the six habitats (Table 2). The two most dominant species (*Tanais dulongi* and *Capitella* "*capitata*") were almost exclusively restricted to the two intertidal habitats, and predominantly in the *Zostera*. Several other species also occurred predominantly in the *Zostera* habitat — *Apseudes australis*, *Leitoscoloplos normalis*, *Pista violacea*, *Platynympha longicaudata*, *Tellina deltoidalis*, *Zeacumantus diemenensis*, *Diplocirrus* sp. and *Scoloplos simplex*. *Nereis bifida* and *Eunice* sp. 1 occurred mainly in the *P. australis* and *P. sinuosa* habitats respectively, while *Asychis* sp. was mainly found in the 5 m subtidal bare habitat. Only four of the dominant species (*Nepthys gravieri*, *Ceratonereis* sp. 1, *Tellina mariae*, and *Scoloplos simplex*) were present in all six habitats. Twenty of the 26 dominants were found in all the subtidal habitats. Thus the dominant species could be separated into two groups: those dominant in the intertidal and those dominant in the subtidal, with few species common to both groups. A detailed analysis of the variability of species composition amongst individual habitats, sites, seasons and sediment characteristics will be presented elsewhere (Ward & Hutchings in prep.).

Comparisons with other areas

Intertidal unvegetated sediments

A recent study by Ainslie *et al.* (1989) of the infauna of intertidal unvegetated mudflats of Northern Spencer Gulf (about 60 km north of our study area) recorded a total of 99 species. These 99 species included 31 species of polychaetes, 31 molluscs, and 22 crustaceans. This is considerably greater than the total of 27 species which were recorded from intertidal unvegetated habitats in this study. The densities of individuals recorded in the Northern Spencer Gulf intertidal habitats (about 550 m^{-2}) was also considerably greater than those recorded in this study (280 m^{-2}). These differences may result from the different scales of sampling in the two studies or to real differences between the locations related to differences in the hydrological conditions between the two Spencer Gulf locations. Similar sampling techniques were used in both studies although Ainslie *et al.* used a 1 mm sized mesh, and 20 replicates were collected at each site in summer and winter from June 1982 to June 1986 inclusive, which is a far greater intensity of sampling than carried out in this study. The Ainslie *et al.* (1989) study sampled a total area of 33 m^2 in Northern Spencer Gulf whereas we sampled about 2 m^2. This difference in total area sampled and the extended temporal scale of the Northern Spencer Gulf study may have contributed to the greater number of species of infauna recorded. Alternatively, the Gulf near Port Pirie may have a depauperate intertidal infauna because of different salinity and temperature regimes.

The species composition of the infauna found by Ainslie *et al.* (1989) in Northern Spencer Gulf is not similar to that found in this study, with very few species being common to both areas. Ainslie *et al.* identified a total of 100 taxa to species level, and in this study we identified 178 taxa to species. Of these only 24 species are common to both Upper and Northern Spencer Gulf. Obviously, some of the taxa identified only to genus may, after further study, be found to occur in both regions. We suggest that this apparent difference in species composition may be related to the different hydrological regimes in these two regions of Spencer Gulf. Northern Spencer Gulf is characterised by high summer salinities, up to 48 ‰ (Nunes & Lennon 1986), and high summer temperatures with wide seasonal fluctuations 11 — 25 °C (Johnson 1981[4]; unpublished data quoted by Ainslie *et al.* 1989). Northern Spencer Gulf is separated from the Upper Gulf by a narrow channel just north of our study area, and this could be responsible for maintaining a different set of hydrological conditions between these two study areas, even though they are close to each other.

Posidonia australis seagrass beds

The low-intertidal seagrass habitat of *Posidonia australis* and *P. sinuosa*, in Northern Spencer Gulf, contained 147 species of infauna with a mean density of about 170 individuals m^{-2} (Ainslie *et al.* 1989). The most similar habitat in our study (*P. australis*) contained 181 species with an average density of 1157 individuals m^{-2}. Ainslie *et al.* do not give any indication of the density of seagrasses in this habitat, but, because *Posidonia* is basically a subtidal seagrass species, we presume that their sample location contained only scattered seagrass on the margins of more substantial subtidal beds of *P. australis*.

P. australis seagrass beds elsewhere in southern Australia have also been studied. In Table 3 the distributions of the major phyla present in *P. australis*

[4]JOHNSON, L. E. (1981) Hydrological data from Upper Spencer Gulf 1975-1978. Fisheries Res. Paper No. 3, 1-30 (Dept Fisheries, Adelaide, SA, unpubl.)

TABLE 3. Posidonia australis: *distribution of the major phyla (S = number of species, d = overall mean density).*

site	Polychaetes	Molluscs	Crustaceans	Echinoderms	Ascidians	Minor	Total
Albany (Hutchings *et al.*, 1991)							
S	47	26	15*	11	11	4	113
d**	731	691	656	132	124	-	2327
Spencer Gulf (this study)							
S	94	34	34	10	3	6	181
d**	883	84	119	37	6	27	1156
NSW (Collett *et al.* 1984)							
S	134	51	106	#	#	32	323
d**	1656	285	710			113	2763

* amphipods not identified to species
# echinoderms and ascidians included in minor phyla
** densities (number of individuals m^{-2}) calculated from total abundances and total area sampled (Albany = 1.2 m^2, Spencer Gulf = 2.014 m^2, NSW = 5.74 m^2).

in Albany, SW West Australia (35°03′27″S 117°03′27″W) (Hutchings *et al.* 1991) and at nine sites along the NSW coast from 32°13′S to 36°54′S (Collett *et al.* 1984) are compared with those occurring in Upper Spencer Gulf. Polychaetes dominated the infauna in these three geographical localities, both in terms of number of individuals and species. The average density of infauna in NSW *Posidonia* beds was twice that of Upper Spencer Gulf, although the NSW data were based on samples totalling 5.74 m^2 in area, collected at nine locations along the NSW coast. Similarly, the *P. australis* sampled in Albany (total area sampled 1.2 m^2) had a mean density of infauna about twice that found in Upper Spencer Gulf in this study.

The species composition of the infauna of *P. australis* in these three geographical areas is different, indicating that although *P. australis* has a wide distribution, occurring from Shark Bay in Western Australia around southern Australia to Wallis Lake on the central coast of NSW (Larkum & den Hartog 1989), the composition and density of its infauna vary according to location. The infauna may also be related to the density of the seagrasses themselves, but at the Upper Spencer Gulf and Albany sites the density and productivity of the *P. australis* beds are similar (Ward 1987; Walker *et al.* 1991). Collett *et al.* (1984) report only a qualitative assessment of the density of seagrass blades which cannot be related to the numeric values determined for the Upper Spencer Gulf and Albany sites. Therefore, because of both different sampling intensities and seagrass densities, it is not possible to directly compare the density or diversity of the infauna found by each of these studies.

In this study we also examined whether the feeding strategies employed by the infauna were similar regardless of geographical location. The fauna was assigned to one of five feeding categories (Table 4) for Upper Spencer Gulf, Albany and the nine locations

TABLE 4. Posidonia australis: *distribution of the fauna amongst feeding categories at Albany, Spencer Gulf and NSW (number of species (%)).*

location	herbivore	suspension	deposit	carnivore	omnivore
Albany (from Hutchings *et al.*, 1991)					
polychaetes	4 (9)	3 (7)	20 (44)	18 (40)	-
molluscs	7 (33)	7 (33)	1 (5)	6 (29)	-
crustaceans	-	-	5 (36)	9 (64)	-
ascidians	-	11 (100)	-	-	-
echinoderms	-	2 (15)	4 (31)	5 (38)	2 (15)
totals	11 (11)	23 (22)	30 (29)	40 (38)	2 (2)
Spencer Gulf (this study)					
polychaetes	11 (12)	12 (13)	40 (43)	30 (32)	1 (1)
molluscs	15 (44)	13 (38)	2 (6)	4 (12)	-
crustaceans	1 (3)	1 (3)	19 (56)	13 (38)	-
ascidians	-	3 (100)	-	-	-
echinoderms	1 (10)	1 (10)	3 (30)	5 (50)	-
totals	27 (16)	30 (17)	64 (37)	52 (30)	1 (1)
NSW (from Collett *et al.*, 1984)					
polychaetes	-	28 (21)	53 (39)	37 (28)	16 (12)
molluscs	10 (19)	24 (47)	7 (14)	4 (8)	1 (2)
crustaceans	3 (3)	4 (4)	28 (26)	20 (19)	44 (41)
totals	13 (5)	56 (19)	88 (30)	61 (21)	61 (21)

along the NSW coast. The designation of feeding categories was determined from the literature (mostly for related species) and from personal observations.

Carnivores, including scavengers, comprised 21 – 38% of the total infauna in a geographical region. The proportion of deposit feeders ranged between 29% (Albany) to 37% (Upper Spencer Gulf). Suspension feeders, which may feed on suspended particulate matter as well as plankton, were between 17 and 22% of the fauna (Table 4). There were major differences in the herbivore and omnivore fauna between locations, with ranges of 5% (NSW) to 16% (Upper Spencer Gulf), and 1% (Upper Spencer Gulf) to 21% (NSW) respectively. These data suggest that the distribution of feeding guilds varies according to geographical location. Perhaps future studies should consider the feeding category of fauna as well as their abundance, productivity and biomass in order to estimate the ecological importance of a species in shallow marine systems. Edgar (1990) used size structure of benthic macrofaunal communities to estimate faunal biomass and secondary productivity but he did not assign the fauna to feeding guilds which may be an additional useful qualitative descriptor for benthic communities.

Posidonia sinuosa seagrass beds

P. sinuosa occurs from Shark Bay to the Great Australian Bight (Larkum & den Hartog 1989). However, the infauna of *Posidonia sinuosa* has only been sampled at one other location in southern Australia – Albany in SW Western Australia (Hutchings *et al.* 1991). The density of the Albany infauna was twice that recorded from Upper Spencer Gulf in this study. This difference between the two faunas was largely the result of higher densities of molluscs, crustaceans and ascidians at Albany (Table 5). Conversely, Upper Spencer Gulf has a considerably increased species richness, the result of an increased number of polychaete species in Upper Spencer Gulf (Table 5). By comparison of the species lists in Hutchings *et al.* (1991) and Appendix 1 of this paper it is clear that there is little similarity in the species composition of the infauna between these two localities. Therefore, as for *P. australis*, the infauna of *P. sinuosa* appears to vary substantially between locations.

Despite the different species composition there was a considerable similarity in feeding types between Upper Spencer Gulf and Albany (Table 6). Deposit feeders, carnivores including scavengers, and

TABLE 5. Posidonia sinuosa: *distribution of the major phyla (S = number of species, d = overall mean density).*

site	Polychaetes	Molluscs	Crustaceans	Echinoderms	Ascidians	Minor	Total
Albany (Hutchings *et al.* 1991)							
S	40	24	18*	7	16	1	106
d**	711	259	611	54	140	-	1797
Spencer Gulf (this study)							
S	97	32	44	12	5	4	192
d**	630	95	76	38	11	11	860

* amphipods not identified to species
** densities (number of individuals m^{-2}) calculated from total abundances and total area sampled (Albany = 1.2 m^2, Spencer Gulf = 2.052 m^2).

TABLE 6. Posidonia sinuosa: *distribution of the fauna amongst feeding categories at Albany and Spencer Gulf (number of species (%)).*

location	herbivore	suspension	deposit	carnivore	omnivore
Albany (from Hutchings *et al.*, 1991)					
polychaetes	3 (7)	6 (13)	18 (39)	19 (41)	-
molluscs	12 (50)	4 (17)	4 (17)	4 (17)	-
crustaceans	-	1 (6)	1 (6)	6 (35)	9 (53)
ascidians	-	14 (100)	-	-	-
echinoderms	-	1 (14)	2 (26)	2 (26)	2 (26)
totals	15 (14)	26 (24)	25 (23)	31 (29)	11 (11)
Spencer Gulf (this study)					
polychaetes	14 (14)	16 (16)	38 (39)	28 (29)	1 (1)
molluscs	9 (28)	12 (38)	3 (9)	8 (25)	-
crustaceans	-	2 (5)	22 (50)	20 (45)	-
ascidians	-	5 (100)	-	-	-
echinoderms	2 (17)	1 (8)	3 (25)	6 (50)	-
totals	25 (13)	36 (19)	66 (35)	62 (33)	1 (1)

suspension feeders were the dominant feeding types in *P. sinuosa* beds in both locations.

Conclusions

While species diversity in the subtidal seagrass beds is higher in Upper Spencer Gulf than in Albany, it is lower than in the seagrass beds of NSW. The density of individuals is far lower in Upper Spencer Gulf than elsewhere, and this may reflect the different temperature and salinity regimes in Upper Spencer Gulf compared to Albany and the nine locations along the NSW coast. Collett *et al.* (1984) concluded that hydrological conditions were important determinants in the composition of the infauna of seagrass beds, and more important than latitudinal effects. This study and the study of Albany (Hutchings *et al.* 1991) indicate that the conclusions of Collett *et al.* (1984) may also hold for the broader geographical region of southern Australia. Hydrological conditions may also be responsible for the difference between the Northern Spencer Gulf intertidal infauna (Ainslie *et al.* 1989) and the intertidal infauna of Upper Spencer Gulf observed in this study.

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Appendix 1 Summary of all data

Species	Family	Habitats						
		intertidal	*Zostera*	*Posidonia australis*	*Posidonia sinuosa*	5m bare	10m bare	sum
Harmothoe sp. 1	Polynoidae			5	7	3	1	16
Harmothoe sp. 2	Polynoidae						1	1
Harmothoe sp. 3	Polynoidae		2		1			3
Paralepidonotus ampulliferus	Polynoidae		1					1
Sigalion sp.	Sigalionidae			1	2	6	3	12
? *Sthenelais* sp.	Sigalionidae						1	1
Chrysopetalum sp.	Chrysopetalidae			1				1
Eumida sp.	Phyllodocidae		21	18	15	5		59
Paranaitis sp.	Phyllodocidae					1	4	5
Pteryosyllis sp. 1	Phyllodocidae						2	2
Phyllodoce sp. A	Phyllodocidae		49	17	4	6		76
*Eteone n.*sp.	Phyllodocidae		9	5	1		1	16
Genetosyllis sp.	Phyllodocidae			1			1	2
Phyllodocid sp. 5	Phyllodocidae		1	4		3		8
Podarke microantennata	Hesionidae			1	2			3
Podarke angustifrons	Hesionidae		11	9				20
Typosyllis sp. 1	Syllidae	1	1	17	3			22
Exogone sp.	Syllidae			2	2			4
Odontosyllis sp. 1	Syllidae				2			2
Odontosyllis sp. 2	Syllidae			2	1			3
Pionosyllis ehlersiaeformis	Syllidae			10	14	2	2	28
Syllinae sp. 2	Syllidae				2		7	9
Typosyllis sp. 2	Syllidae			52	20	1	1	74
Ehlersia sp.	Syllidae			15	22	1	1	39
Syllinae sp. 8	Syllidae			1				1
Ceratonereis mirabilis	Nereididae	1	6	14	3	4	4	32
Neanthes sp. 1	Nereididae		1			1	7	9
Neanthes bassi	Nereididae		10	15	3	2	13	43
Nereis bifida	Nereididae		31	577	29	7	1	645
Neanthes kerguelensis	Nereididae		6	9	56		3	74
Platynereis sp.	Nereididae		65	5	2	1		73
Neanthes sp. 3	Nereididae		1		7			8
Neanthes vaalii	Nereididae	45		1	1	1	1	49
*Ceratocephela n.*sp. 1	Nereididae					1		1
Neanthes sp. 2	Nereididae				1			1
Ceratonereis sp. 1	Nereididae	248	8	34	14	69	11	384
Ceratonereis aequisetis	Nereididae		4					4
Nereid sp. 20	Nereididae			2	1			3
Gymnonereis sp. 1	Nereididae					2		2
Nephtys gravieri	Nephytidae	109	99	13	115	139	67	542
Glycera americana	Glyceridae		3	2	5	5	3	18
Glycinde sp. 1	Glyceridae		31	12	9	4	3	59
Goniada maculata	Goniadidae					1		1
Onuphid sp. 1	Onuphidae		1	13	21	1		36
Nematonereis unicornis	Eunicidae			103	118	25	7	253
Eunicid juv sp. 1	Eunicidae				1			1
Marphysa sp. 1	Eunicidae	1		1	2	3	34	41
Marphysa sp. 2	Eunicidae	2	15	1	2	2		22
Lysidice sp. 1	Eunicidae			1	5			6
Eunice sp. 1	Eunicidae			5	81	19	4	109
Eunice sp. 3	Eunicidae			41	72	51	35	199
Eunice sp. 4	Eunicidae			7		6	2	15
Eunice sp. 6	Eunicidae			1	14	39	8	62
Eunice sp. 9	Eunicidae						3	3
Eunicid sp. 11	Eunicidae				1			1
Eunice sp. 5	Eunicidae			5	2	6		13
Augeneria verdis	Lumbrineridae		131	18	48	26	16	239
Lumbrineris sp. 1	Lumbrineridae		8	1	4	4	2	19
Arabella sp. 1	Arabellidae			9	8	11	3	31
Schistomeringos sp. 1	Dorvilleidae					7	1	8
Schistomeringos loveni	Dorvilleidae		19	16	6	16	7	64
Leitoscoloplos sp. 1	Orbiniidae			5	1	1		7
Phylo sp. 1	Orbiniidae			1	5			6
Naineris grubei australis	Orbiniidae			4	6			10

Appendix 1 Summary of all data (continued)

Species	Family	Habitats						
		intertidal	*Zostera*	*Posidonia australis*	*Posidonia sinuosa*	5m bare	10m bare	sum
Scoloplos simplex	Orbiniidae	1	74	17	4	4	1	101
Leitoscoloplos normalis	Orbiniidae	31	414	121	13	1		580
Family Orbiniidae	Orbiniidae		17	1			1	19
Aonides oxycephela	Spionidae						1	1
Spio sp. B	Spionidae			2			1	3
Prionospio sp. 2	Spionidae		1	2		1		4
Polydora sp. 1	Spionidae		2					2
Pseudopolydora sp. 1	Spionidae	5		1		4		10
Boccardia sp. 3	Spionidae						1	1
Boccardia sp. 2	Spionidae			1				1
Aquilaspio multipinnulata	Spionidae		7	1	9	1	2	20
Aquilaspio aucklandica	Spionidae		3			2	3	8
Spio pacifica	Spionidae				1			1
Scolelepis sp. 2	Spionidae				5	17	5	27
Pseudopolydora sp. 4	Spionidae					1	5	6
Malacoceros sp. 1	Spionidae			10	28	38	14	90
Scolelepis sp. 1	Spionidae				2	4		6
Spionidae sp. 2	Spionidae				1	1		2
Spionidae sp. 3	Spionidae		1				1	2
Boccardia sp. 1	Spionidae				1			1
Aricidea sp. 2	Pilargiidae		1	1	3	1		6
Magelona sp. 1	Magelonidae			2	5	1	1	9
Tharyx sp. 2	Cirratulidae			1				1
Caulleriella sp. 1	Cirratulidae				4	1		5
Caulleriella sp. 2	Cirratulidae		1	20	14	31	6	72
Caulleriella sp. 3	Cirratulidae		7	35	43	14	1	100
Caulleriella sp. 4	Cirratulidae		20	31	38	21	3	113
Cirriformia sp. 1	Cirratulidae		43	43	28	4	9	127
Cirriformia sp. 2	Cirratulidae		29	43	13	5	2	92
Cirratulid sp. 1	Cirratulidae		3	1	4	1		9
Diplocirrus sp.	Flabelligeridae		92	3	4	1	2	102
Scalibregma inflatum	Scalibregmatidae			5	2	11	2	20
Hyboscolex dichranochaetus	Scalibregmatidae			1				1
Armandia intermedia	Opheliidae		10	51	5	8		74
Heteromastus filiformis	Capitellidae		26	5				31
Capitella "capitata"	Capitellidae	53	608					661
Barantolla sp.	Capitellidae		88	57	88	46	6	285
Mediomastus n. sp.	Capitellidae		19	19	36	7	7	88
?Scyphoproctus sp. 1	Capitellidae		1		1	5	1	8
Scyphoproctus sp. 2	Capitellidae			7	2	7	1	17
Notomastus sp. 1	Capitellidae		2	96	51	25	12	186
Notomastus torquatus	Capitellidae			4	14	29	16	63
Leiochrides sp. 1	Capitellidae					3	1	4
Poecilochaetous serpens	Poecilochaetidae		1			2	8	11
Asychis sp.	Maldanidae			5	2	115	19	141
Petaloproctus sp.	Maldanidae		1	10	2	10	1	24
Praxillella sp.	Maldanidae			1	2	2		5
Maldanid sp. 3	Maldanidae						3	3
Owenia fusiformis	Oweniidae					5	3	8
Pectinaria sp. 1	Pectinaridae				1		3	4
Isolda pulchella	Ampharetidae					1	1	2
Ampharetid sp. 1	Ampharetidae			1	3	38	7	49
Ampharetid sp. 3	Ampharetidae				1			1
Lysilla pacifica	Terebellidae			11	4	4	7	26
Polycirrus sp. 1	Terebellidae			1			1	2
Polycirrus tesselatus	Terebellidae		4	5	26	1	3	39
Polycirrus cf. nephrosus	Terebellidae			1				1
?Decathelepus	Terebellidae						1	1
Thelepus plagiostoma	Terebellidae				1	2		3
Thelepus extensus	Terebellidae						1	1
Streblosoma sp.	Terebellidae					33	24	57
Lanassa exelysis	Terebellidae			6	18		1	25
Lysilla laciniata	Terebellidae			2	1		1	4
Pista australis	Terebellidae		18	16	11	6	12	63
Pista violacea	Terebellidae		440	6	12	3	12	473

Appendix 1 Summary of all data (continued)

Species	Family	Habitats						
		intertidal	*Zostera*	*Posidonia australis*	*Posidonia sinuosa*	5m bare	10m bare	sum
Neoleprea sp.	Terebellidae			4	8	3		15
Loimia ingens	Terebellidae					2		2
Lanassa ocellata	Terebellidae			7	2			9
Eupolymnia koorangi	Terebellidae		24	26	3	1	2	56
Nicolea amnis	Terebellidae		2		7		1	10
Lanicides fascia	Terebellidae						1	1
Amphitritinae sp. 3	Terebellidae			1		1		2
Amphitritinae sp. 4	Terebellidae					2		2
Terebellides stroemii	Trichobranchidae			7	6	5	1	19
Trichobranchus sp.	Trichobranchidae	1		4	4	1		10
Sabellid sp. 1	Sabellidae		87		1	3		91
Euchone variabilis	Sabellidae			2	5	2	4	13
Laonome sp. 1	Sabellidae						2	2
Sabellid sp. 3	Sabellidae				2	6	10	18
Sabellid sp. 4	Sabellidae						1	1
Galeolaria sp.	Serpulidae				3			3
Serpula sp. 2	Serpulidae			1				1
Serpula sp. 1	Serpulidae						1	1
Hydroides sp. 1	Serpulidae		10	4	7	4	1	26
total	**polychaetes**	498	2590	1779	1292	1029	497	7685
Haliotis sp.	Haliotidae				1			1
Amblychilepas nigrita	*Fissurellidae*		*16*	*1*				*17*
Amblychilepas cf. oblonga	Fissurellidae		1					1
Amblychilepas sp.	Fissurellidae		1					1
Emarginula sp.	Fissurellidae			1				1
Collisella sp.	Lotiidae		1					1
Naccula parva	Lotiidae			5	10			15
Isoclanculus dunkeri	Trochidae		2	3	4			9
Phasianotrochus cf. apicinus	Trochidae			3	1			4
Thaliotia sp.	Trochidae			1				1
Gena sp.	Trochidae					1		1
Micrastrea rutidoloma	Turbinidae		1	4	4			9
Phasianella australis	Turbinidae			1		1		2
Bembicium vittatum	Littorinidae		1					1
Triphorid sp. 1	Triphoridae					1	1	2
Zeacumantus diemenensis	Potamididae	1	206					207
Bittium sp. 1	Cerithiidae			2	1			3
Bittium sp. 2	Cerithiidae					4	1	5
Diala sp.	Dialidae			1	3	1		5
Gazameda iredalei	Turritellidae				2		1	3
Sabia conica	Hipponicidae		1			1		2
Zeacrypta immensa	Calyptraeidae						7	7
Sigapatella calyptraeformis	Calyptraeidae						3	3
Eunaticina umbilicata	Naticidae		2		2			4
Ectosinum zonale	Naticidae						1	1
Cominella eburnea	Buccinidae		2	1	2	2		7
Cominella sp.	Buccinidae				1			1
Nassarius pauperus	Nassariidae				1			1
Fusinus australis	Fasciolariidae					1	1	2
Dentimitrella cf. lincolnensis	Columbellidae			2	1			3
Splendrilla harpularia	Turridae				2			2
Conus anemone	Conidae			1	1			2
Scaeoleda verconis	Nuculidae						3	3
Solemya cf. australis	Solemyidae				1	16		17
Barbatia pistachia	Arcidae						2	2
Glycymeris flammea	Glycymeridae						1	1
Glycymeris radians	Glycymeridae				8			8
Limopsis cf. tenisoni	Limopsidae					1	5	6
Limopsis sp.	Limopsidae						5	5
Mytilus sp.	Mytilidae					3		3
Austromytilus penetectus	Mytilidae		5	2	2	57	211	277
Trichomya hirsuta	Mytilidae						3	3
Musculus cf. ulmus	Mytilidae		2	2	1	4	6	15
Musculus cf. paulucciae	Mytilidae			3	2	2	10	17
Modiolus albicostatus	Mytilidae						1	1

Appendix 1 Summary of all data (continued)

Species	Family	Habitats						
		intertidal	*Zostera*	*Posidonia australis*	*Posidonia sinuosa*	5m bare	10m bare	sum
Brachydontes erosus	Mytilidae		8	3		1		12
Atrina tasmanica	Pinnidae					1		1
Atrina sp.	Pinnidae						2	2
Pinna bicolor	Pinnidae					5	1	6
Electroma georgiana	Pteriidae		11	5	2	3	3	24
Electroma sp.	Pteriidae						2	2
Malleus meridianus	Malleidae					3	1	4
Vulsella vulsella	Malleidae			7				7
Equichlamys bifrons	Pectinidae					1	2	3
Lima nimbifer	Limidae						1	1
Monia lone	Anomiidae			1		18		19
Monia zelandica	Anomiidae						4	4
Anomia descripta	Anomiidae					2	2	4
Saccostrea "australis"	Ostreidae			1	3	3	19	26
Wallucina assimilis	Lucinidae	4	60	2	5	4		75
Cavitidens perplexa	Lucinidae		4	29	14	1	1	49
Myrtea bractea	Lucinidae				1			1
Venericardia sp.	Carditidae					1	1	2
Fulvia tenuicostata	Cardiidae					1		1
Chama ruderalis	Chamiidae						1	1
Dosinia histrio	Veneridae						1	1
Circe rivularis	Veneridae			1		1	3	5
Katelysia rhytiphora	Veneridae		2	11		15		28
Katelysia sp.	Veneridae	1	5				1	7
Placamen flindersi	Veneridae						13	13
Timoclea sp.	Veneridae			1	1	3	1	6
Mactra sp.	Mactridae			1			2	3
Tellina mariae	Tellinidae	6	71	20	45	12	18	172
Tellina deltoidalis	Tellinidae		226		8	5		239
Tellina sp. 1	Tellinidae						1	1
Tellina sp. 2	Tellinidae						7	7
Semele monilis	Semelidae						2	2
Laternula creccina	Laternulidae	11	48			2	6	67
Myadora complexa	Myochamidae				1	2	4	7
Frenamya patula	Pandoridae						1	1
Teredo	Teredinidae			2				2
Bivalve 2							1	1
Bivalve 4							2	2
Chiton sp. 1	Ischnochitonidae					1	2	3
Stenochiton longicymba	Ischnochitonidae			38	46			84
Stenochiton cf. pilsbryanus	Ischnochitonidae			10	17	2	1	30
Chiton sp. 2	Ischnochitonidae						1	1
Chiton sp. 3	Ischnochitonidae					2	4	6
Dorid sp. 1	Doridiidae			2				2
Dorid sp. 2	Doridiidae			1				1
Dorid sp. 3	Doridiidae		1					1
Philinopsis lineolata	Aglajidae						1	1
Philine sp.	Philinidae				1	1		2
Atys sp.	Haminoeidae			1				1
Salinator sp.	Amphibolidae	2						2
total	molluscs	25	677	169	194	185	374	1624
Nebaliidae sp. 1	Leptostracan			19	6			25
Paguroidea sp. 1				3	1		1	5
Grapsidae sp. 2	Grapsidae				1			1
Hemigrapsus spinosus	Grapsidae	1	31	2	2		1	37
Halicarcinus rostratus	Hymenosomatidae					1	3	4
Halicarcinus ovatus	Hymenosomatidae			2				2
Portunus pelagicus	Portunidae		1					1
Ebalia intermedia	Leucosiidae					3	3	6
Ebalia sp. A	Leucosiidae		2					2
Macrobrachium intermedium	Palaemonidae		9		2		2	13
Alpheus bidens	Alpheidae			4				4
Alpheus euphrosyne richardsoni	Alpheidae		2					2
Alpheus novaezealandiae	Alpheidae			2				2

Appendix 1 Summary of all data (continued)

Species	Family	Habitats						
		intertidal	*Zostera*	*Posidonia australis*	*Posidonia sinuosa*	5m bare	10m bare	sum
Alpheus sp.	Alpheidae		1					1
Metapenaeopsis novaeguineae	Penaeidae					1		1
Apseudes australis	Apseudidae		513	63	2	7	3	588
Apseudes sp. 1	Apseudidae		5		3	4	2	14
Apseudes sp. 2	Apseudidae		72	8	3			83
Kalliapseudes sp.	Apseudidae						1	1
Tanais dulongi	Tanaidae	26	819				1	846
Leptochelia ignota	Tanaidae		1	1			2	4
Cymadusa sp.	Amphithoidae	2	5	24	13			44
Ampithoidae sp. 1	Ampithoidae				2			2
Ampelisca toora	Ampeliscidae				2	1	1	4
Byblis cf. bega	Ampeliscidae					1		1
Protolembos drummondae	Aoridae			17	22	3		42
Xenocheira fasciata	Aoridae					2		2
Bemlos strigilis	Aoridae			1				1
Ceradocus ramsayi	Melitidae				1		1	2
Maera mastersi	Melitidae			6	1	2		9
Maera sp.	Melitidae		1		2			3
Ceradocus dooliba	Melitidae				6			6
Ceradocus rubromaculatus	Melitidae					2		2
Ceradocus serratus	Melitidae			1		2		3
Cottesloe berringar	Melitidae			6	1			7
?Parelasmopus sp.	Melitidae			12	1			13
Melitidae sp. 1	Melitidae			1				1
Melitidae sp. 2	Melitidae			1				1
Melitidae sp. 4	Melitidae			3				3
Leucothoe ?commensalis	Leucothidae				1			1
Leucothoe assimilis	Leucothoidae				1			1
Leucothoe sp. 2	Leucothoidae						1	1
Leucothoe sp. 1	Leucothoidae						2	2
Waldeckia sp. 1	Lysianassidae					1		1
Waldeckia sp. 2	Lysianassidae					1		1
Waldeckia sp. 3	Lysianassidae			1				1
Parawaldeckia sp.	Lysianassidae				1			1
Tryphosella sp.	Lysianassidae				1			1
Ischyroceridae sp. 1	Ischyroceridae			3	5			8
Phoxocephalidae spp.	Phoxocephalidae			1	23	5	4	33
Atylus sp.	Dexaminidae				4			4
Paradexamine lanacoura	Dexaminidae				1	1		2
Paradexamine ?linga	Dexaminidae			1	2			3
Paradexamine moorehousei	Dexaminidae			1				1
Oedicerotid sp. 1	Oedicerotidae				1	1		2
Eusirid sp. 1	Eusiridae				1			1
Eusirid sp. 2	Eurisidae			2				2
Eusirid sp. 3	Eusiridae				1			1
Eusirid sp. 4	Eusiridae			1	3			4
Hyale sp.	Hyalidae		43					43
Tomituka doowi	Platyischnopidae				1			1
Natatolana wowine	Cirolanidae				6	12	3	21
Platynympha longicaudata	Sphaeromatidae	2	291	22	8			323
Cymodoce sp. 1	Sphaeromatidae					1		1
Cymodoce sp. 2	Sphaeromatidae	2	49	18	9			78
Cymodoce bidentata	Sphaeromatidae				1			1
Limnoria sp. nov.	Limnoriidae			1	5			6
Euidotea peronii	Idoteidae		4					4
Crabyzos longicaudatus	Idoteidae				1			1
Euidotea bakeri	Idoteidae		7					7
Leptanthura diemenensis	Paranthuridae					1		1
Accalathura bassi	Paranthuridae			2	1			3
Mesanthura stypandra	Anthuridae			1				1
Amakusanthura olearia	Anthuridae		3		1			4
Apanthura cf. *isotoma*	Anthuridae				1			1
Haliophasma sp. 1	Anthuridae		3	3	3	1		10
Callianassa sp.	Callianassidae					1	6	7
Gomeza bicornis	Corystidae				2	4		6

Appendix 1 Summary of all data (continued)

Species	Family	Habitats						
		intertidal	*Zostera*	*Posidonia australis*	*Posidonia sinuosa*	5m bare	10m bare	sum
Ceratoplax punctata	Goneplacidae			4				4
Litocheira bispinosa	Goneplacidae			3	1			4
Actumnus setifer	Pilumnidae						1	1
total	**crustaceans**	33	1862	240	156	58	38	2387
Ascidiidae sp. 1	Ascidiidae		18			2		20
Ascidiidae sp. 2	Ascidiidae		3	1				4
Ascidiidae sp. 3	Ascidiidae				1	1	16	18
Ascidiidae sp. 4	Ascidiidae				5	1		6
Ascidiidae sp. 5	Ascidiidae				1			1
Ascidiidae sp. 6	Ascidiidae					2		2
Microcosmus sp. 1	Pyuridae		3	10	11	2		26
Didemnid sp. 1	Didemnidae		1					1
Pyura stolonifera	Pyuridae			1	4	20	6	31
Polycarpa ?pedunculata	Ascidiacea					4		4
total	**ascidians**	0	25	12	22	32	22	113
Pentacta ignava	Cucumariidae				1			1
Cucumella mutans	Phyllophoridae				1			1
Thyone sp.	Phyllophoridae						1	1
Scoliorhapis sp. ?nov.	Chiridotidae			1	5	5	1	12
Trochodota shepherdi	Chiridotidae			1			3	4
Leptosynapta dolabrifera	Synaptidae		74	42	33		1	150
Order Synaptid	Synaptidae			3				3
Thymio sycia	Holothuriidae			1				1
Goniocidaris tubaria	Cidaridae						1	1
Temnopleurus michaelseni	Temnopleuridae				1	3	14	18
Tosia australis	Goniasteridae			1	3			4
Patiriella exigua	Asterinidae		1					1
Amphipholis squamata	Amphiuridae		5	2		3	1	11
Amphiura elandiformis	Amphiuridae				1	1	23	25
Amphiura parviscutata	Amphiuridae			10	4	12	20	46
Amphiura (Fellaria) sp.	Amphiuridae				2	1		3
Amphiura trisacantha	Amphiuridae			3	9		1	13
Amphiura sp.	Amphiuridae	1		10	15	1		27
Ophiocentrus pilosus	Amphiuridae				3	1		4
Ophioconis opacum	Ophiodermatidae					1		1
total	**echinoderms**	1	80	74	78	28	66	327
Syngnathus phillipi	Syngnathidae		3					3
Favonigobius lateralis	Gobiidae		4					4
Pseudogobius olorum	Gobiidae		2					2
Callogobius mucosus	Gobiidae			5				5
Heteroclinus sp.					1			1
Ophiclinops varius					1			1
Gymnapistes marmoratus	Scorpaenidae		4					4
Platycephalidae				1				1
Vanacampus sp.			1					1
Nemertean	Nemertean		6	5	1	3	2	17
Enteropneust							5	5
Pycnogonid				2				2
Hirudinea				1				1
Sipunculan		1	10	41	19	14	11	96
insects		16						16
Porifera sp. 1							2	2
Porifera sp. 2			98					98
Porifera sp. 3						1		1
total	**minor taxa**	17	128	55	22	18	20	260
Total		574	5362	2329	1764	1350	1017	12396

SEVENTEEN NEW SPECIES OF AUSTRALIAN BUPRESTIDAE (INSECTA: COLEOPTERA) AND A HOST PLANT OF *CASTIARINA UPTONI* (BARKER).

*BY S. BARKER**

Summary

Sixteen new species of *Castiarina* are described: *C. aeruginosa* sp. nov., *C. antia* sp. nov., *C. anthrene* sp. nov. *C. chrysothoracica* sp. nov., *C. crucianella* sp. nov., *C. hasenpuschi* sp. nov., *C. indigesta* sp. nov., *C. luteofusca* sp. nov., *C. markhanloni* sp. nov., *C. melasma* sp. nov., *C. mimesis* sp. nov., *C. nebula* sp. nov., *C. rayclarkei* sp. nov., *C. tenebrosa* sp. nov., *C. woodi* sp. nov. and *C. xystra* sp. nov.; and one new species of *Themognatha, T. gordonburnsi* sp. nov. *Dicrastylis georgei* Munir is identified as a host plant of *C. uptoni* (Barker).
KEY WORDS: Coleoptera, Buprestidae, new species, *Castiarina, Themognatha.*

Transactions of the Royal Society of S. Aust. (1993), **117**(1), 15-26.

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by S. BARKER*

Summary

BARKER, S. (1993) Seventeen new species of Australian Buprestidae (Insecta: Coleoptera) and a host plant of *Castiarina uptoni* (Barker). *Trans. R. Soc. S. Aust.* **117**(1), 15-26 4 June, 1993.

Sixteen new species of *Castiarina* are described: *C. aeruginosa* sp. nov., *C. antia* sp. nov., *C. anthrene* sp. nov. *C. chrysothoracica* sp. nov., *C. crucianella* sp. nov., *C. hasenpuschi* sp. nov., *C. indigesta* sp. nov., *C. luteofusca* sp. nov., *C. markhanloni* sp. nov., *C. melasma* sp. nov., *C. mimesis* sp. nov., *C. nebula* sp. nov., *C. rayclarkei* sp. nov., *C. tenebrosa* sp. nov., *C. woodi* sp. nov. and *C. xystra* sp. nov.; and one new species of *Themognatha*, *T. gordonburnsi* sp. nov. *Dicrastylis georgei* Munir is identified as a host plant of *C. uptoni* (Barker).

KEY WORDS: Coleoptera, Buprestidae, new species, *Castiarina*, *Themognatha*.

Introduction

The search for new species of Buprestidae occurring irregularly in isolated areas has been continued, with some success, by a group of dedicated amateur entomologists. Included in this new material are specimens of species rare in collections and some new species which are described herein as are some new species from older series which have been made available to me.

The major gap in knowledge of this family in Australia is information on their larval biology and food plants. *Castiarina uptoni* (Barker) occurs in very isolated arid areas of the country. The larval food plant of the population which occurs in the Ashburton River district in W.A. has been identified as *Dicrastylis georgei* Munir.

Gardner (1989a) in a generic revision of the tribe Stigmoderini pointed out that *Polychroma* Dejean held date priority over *Castiarina* LaPorte & Gory, but had not been used for over 130 years. She subsequently applied to the ICZN to have the name *Castiarina* conserved (Gardner 1989b) and that action has now been taken (Opinion 1628, Bull. Zool. Nomencl. 48 (1) March 1991, pp. 74-75).

Materials and Methods

Collection date and locality information listed for each specimen is a copy of all data written on each individual label. Male genitalia were prepared and displayed by the method described by Barker (1987) referred to in the text and if previously published, reference is given to the publication date. The specimens illustrated in all species but two are the holotype. Two allotypes are illustrated and the fact noted in the appropriate *remarks* section. Measurements given are mean total body length and width with standard error, except where there are insufficient specimens available to make the last calculation, when only mean is given. Acronyms used in the text for museum and private collections following the four letter system of Watt (1979) are: ANIC Australian National Insect Collection, Canberra; NMVA National Museum of Victoria, Melbourne; SAMA South Australian Museum, Adelaide; WAMA Western Australian Museum, Perth; RCBA Mr R. Clarke, Byron Bay; JHIQ Mr J. Hasenpusch, Innisfail; MHSA Mr T. M. S. Hanlon, Sydney; MPWA Mr M. Powell, Melville; RMNA Mr R. Mayo, Wallsend; ASSA, Mr A. Sundholm, Sydney; GWQA, Mr G. Wood, Atherton.

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Castiarina crucianella sp. nov.

FIGS 1C, 2B

Holotype. ♂, 136 km NE Paynes Find, W.A., 31.ix.1984, Jones & Powell, WAMA.

Allotype. ♀, same data as holotype, WAMA.

Paratypes. W.A.: 2♂♂, 3♀♀, same data as holotype, SAMA, MPWA.

Colour. Head, antennae and pronotum blue-grey. Scutellum blue. Elytra orange with following blue markings: narrow basal margin; premedial fascia not reaching margin, reduced to elongate oblique mark in some specimens; post-medial fascia reaching margin; apical mark, all marks connected along suture. Ventral surface and legs blue. Hairs silver.

Shape and sculpture. Head closely punctured, median sulcus broad, muzzle short. Antennae, antennomeres: 1-3 obconic; 4-11 toothed. Pronotum closely punctured, narrow basal fovea extending forwards to middle as glabrous line, basal notches represented by glabrous area on each side more marginal than medial; apical margin straight, basal margin bisinuate; laterally parallel-sided at base, rounded to widest pre-medially, rounded and narrowed to apex. Scutellum scutiform, glabrous, excavate. Elytra punctate-striate, intervals convex, smooth, laterally angled out from base, rounded at humeral callus, medially concave, rounded post-medially and narrowed to bispinose apex; sharp

Fig. 1. Photomicrographs of male genitalia of the following *Castiarina* spp.: A. *C. militaris* (Carter); B. *C. xystra* sp.nov.; C. *C. crucianella* sp.nov.; D. *C. aeruginosa* sp.nov.; E. *C. sanguinolenta* (C & G); F. *C. mimesis* sp.nov.; G. *C. inconspicua* (Saunders); H. *C. markhanloni* sp.nov.; I. *C. antia* sp.nov.; J. *C. guttifera* (Obenberger); K. *C. tenebrosa* sp.nov.; L. *C. hasenpuschi* sp.nov.; M. *C. luteofusca* sp.nov.; N. *C. woodi* sp.nov.; O. *C. nebula* sp.nov.; P. *C. analis* (Saunders); Q. *C. indigesta* sp.nov.; R. *C. rollei* (Kerremans); S. *C. rayclarkei* sp.nov.; T. *C. chrysothoracica* sp.nov. and *Themognatha*: U. *T. gordonburnsi* sp.nov.

marginal spine, smaller sutural spine, margin rounded and indented between spines, apices diverging slightly. Ventral surface with shallow punctures, hairy, hairs medium length, edges of abdominal segments glabrous. S7: truncate, medially indented in both sexes. Size. Males, 4.7 × 13.1 mm (3). Females 5.2 × 13.4 mm (4).

Male genitalia. (Fig. 1C) Parameres diverging from basal piece, more so post-medially, rounded to apex. Median lobe pointed, sides obtusely angled away. Apophysis of basal piece medium width, rounded apically.

Remarks. Resembles *C. crux* (Saunders) and *C. nota* Barker. Differs from those species by being larger, with bright blue markings and different male genitalia (Barker 1990: Figs 1K, 1L). Name derived from *crux* L., cross.

Castiarina aeruginosa sp. nov.
FIGS 1D, 2A

Holotype. ♂, 17 km E Mt Carbine, Qld, 23.i.1991, J. Hasenpusch & S. Barker, SAMA I 21,241.
Allotype. ♀ Brumby Gulley, Mareeba-Kuranda Rd, Qld, 4.i.1981, S. Barker, SAMA I 21,242.
Paratypes. Qld: 1♂ 1♀, Mt Molloy, 26.xii.1985, A. Walford-Huggins, SAMA. W.A.: 1♂, 1♀, 12 km E Broome, 5.iv.1986, D. Knowles, MPWA.
Colour. Head coppery-green. Antennae purple. Pronotum and scutellum coppery-green. Elytra pale yellow with following green markings: narrow basal margin; variable post-medial spot at margin on each elytron; apical mark. Ventral surface: sternum coppery-green, abdomen pale yellow. Legs purple. Hairs silver.
Shape and sculpture. Head closely punctured, median sulcus broad, muzzle short. Antennae, antennomeres: 1-3 obconic; 4-11 toothed. Pronotum closely punctured laterally, less so medially, basal fovea, basal notches more marginal than medial; apical margin projecting medially, basal margin barely bisinuate; laterally angled inwards from base, rounded to widest pre-medially, rounded and narrowed to apex. Scutellum scutiform, glabrous, flat. Elytra punctate-striate, intervals convex, shallowly punctured; laterally angled out from base, rounded at humeral callus, medially concave, rounded post-medially and narrowed to bispinose apex; small marginal spine, very small sutural spine, margin rounded and indented between spines, apices diverging slightly, apical margin subserrate. Ventral surface with shallow punctures moderately hairy, hairs short, edges of abdominal segments glabrous. S7: males truncate; females rounded, slightly indented medially.

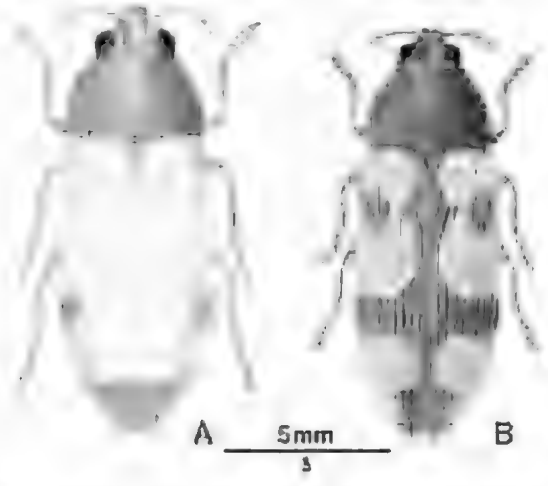

Fig. 2. Habitus illustrations of the following *Castiarina* species. A. *C. aeruginosa* sp.nov. holotype; B. *C. crucianella* sp.nov. holotype.

Size. Males, 4.3 × 11.2 mm (3). Females, 5.1 × 13.5 mm (3).
Male genitalia. (Fig. 1D). Short and broad. Parameres angled away from basal piece, more so post-medially, rounded to apex. Median lobe sharp, sides obtusely angled away; Apophysis of basal piece medium width, rounded at apex.

Remarks. This species resembles *C. straminea* (Saunders) but distinguished by greenish reflections of coppery markings and is smaller species, male genitalia differ (Barker 1986: Fig. 2N) and has northern distribution in Qld and W.A.. *C. straminea* occurs in central and southern Qld and northern N.S.W. Name derived from *aerugo* L., verdigris.

Castiarina chrysothoracica sp. nov.
FIGS 1T, 4B

Holotype. ♂, Mt Carbine, Qld, 15.i.1991, R. Clarke, SAMA I 21,243.
Allotype. ♀, same data as holotype, SAMA I 21,244.
Paratypes. Qld: 2♀ ♀, Mt Carbine, 8.i.1992, R. Clarke, RCBA; 1♂, Mt Garnet, 9.i.1992, R. Clarke, MHSA; 1♂, same data as holotype, RCBA; 2♂ ♂, Mt Carbine, 16.i.1991, R. Clarke, RCBA; 1♂, Mt Carbine, 8.i.1992, R. Clarke, RMNA.
Colour. Head and antennae green with yellow reflections. Pronotum green with golden reflections. Scutellum green with yellow reflections. Elytra yellow with the following markings: blue-green narrow basal margin and medial V-shaped mark surrounding scutellum; blue post-medial fascia reaching margin; blue apical mark, last two marks narrowly connected along suture. Ventral surface: sternum green with yellow reflections; male abdomen testaceous; female abdomen green except apex S7 testaceous. Legs green. Hairs silver.
Shape and sculpture. Head closely punctured, median sulcus broad, muzzle short. Antennae, antennomeres: 1-3 obconic; 4-11 toothed. Pronotum closely punctured, narrow basal fovea extending forwards to middle as glabrous line, basal notches more marginal than medial; apical margin slightly projecting medially, basal margin almost straight; laterally angled outwards from base, rounded pre-medially, tapered to apex. Scutellum scutiform, glabrous, excavate. Elytra punctate-striate, intervals convex, punctured; laterally angled out from base, rounded at humeral callus, medially concave, rounded post-medially and narrowed to bispinose apex; sharp marginal spine, smaller sutural spine, margin rounded and indented between spines, apices diverging, apical margin subserrate. Ventral surface with shallow punctures, moderately hairy, hairs short, edges of abdominal segments glabrous. S7: rounded in both sexes.
Size. Males, 14.3 ± 0.24 × 5.5 ± 0.12 mm (6). Females, 13.5 × 5.1 mm (3).

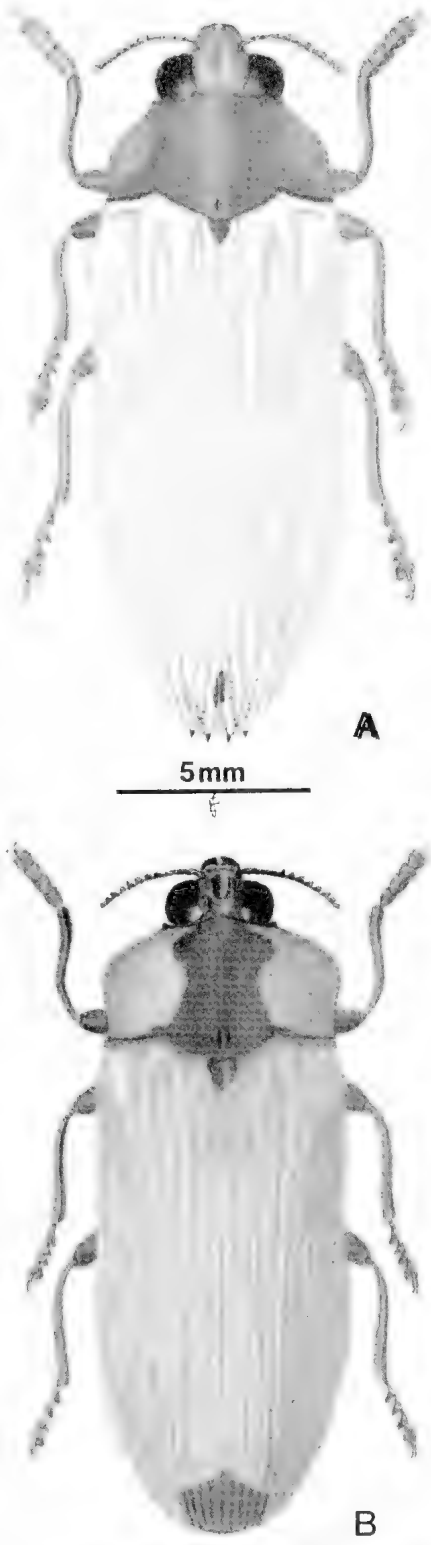

Fig. 3. Habitus illustrations of the following *Castiarina* species: A. *C. rayclarkei* sp.nov. holotype; B. *C. indigesta* sp.nov. holotype.

Male genitalia. (Fig. 1T) Parameres slightly angled outwards from basal piece, slightly rounded medially, rounded at apex. Median lobe sharp, sides obtusely angled away. Apophysis of basal piece short and broad, rounded apically.

Remarks. Colour and pattern of male resemble those of *C. garnettensis* (Barker) but that species has spineless apex and male genitalia are different (Barker 1989: Fig. 1G). Name derived from *chrysos* Gr., gold and *thorax* Gr., chest.

Castiarina melasma sp. nov.
FIG. 4D

Holotype. ♀, Milmerran, Qld, 1.xii.1990, R. Clarke, SAMA I 21,245.
Paratypes. Qld: 2♀♀, Milmerran, 7.xii.1990, R. Clarke, RCBA.
Colour. Head, antennae, pronotum and scutellum green with yellow reflections. Elytra yellow with black apical mark. Ventral surface and legs green. Hairs silver.
Shape and sculpture. Head closely punctured, median sulcus narrow, muzzle short. Antennae, antennomeres: 1-3 obconic; 4-11 toothed. Pronotum closely punctured, basal fovea extending to middle as impressed line, basal notches on each side more marginal than medial; apical margin projecting medially, basal margin barely bisinuate; laterally parallel-sided at base, angled inwards then rounded to widest pre-medially, rounded and narrowed to apex. Scutellum narrow, scutiform, glabrous, excavate. Elytra punctate-striate, intervals convex, flat, punctured; laterally angled outwards from base, rounded at humeral callus, medially concave, rounded post-medially and narrowed to bispinose apex; small, sharp marginal spine, very small sutural spine, margin rounded and indented between spines, apices hardly diverging, apical margin subserrate. Ventral surface with shallow punctures, moderately hairy, sternal hairs medium length, abdominal hairs very short, edges of abdominal segments glabrous. S7: male unknown; female truncate and indented medially.
Size. Females, 13.7 × 5.3 mm (3).

Remarks. Structure, colour and pattern distinct. Name derived from *melasma* Gr., a black spot.

Castiarina indigesta sp. nov.
FIGS 1Q, 3B

Holotype. ♂, Kuranda, Qld, 2.ii.1992, J. Hasenpusch, SAMA I 21,246.
Allotype. ♀, Davies Creek, Mareeba, Qld, 18.i.1991, S. Barker, SAMA I 21,247.
Paratypes. Qld: 2♂♂, 1♀, Kuranda, i.1948, G. Brooks, ANIC; 5♂♂, 1♀, Kuranda, F. P. Dodd, SAMA; 1♂, Kuranda, 10.i.1980, G. Wood, RMNA; 1♀, Mt Molloy, ii.1987, G. Wood, RMNA; 1♂. Mt

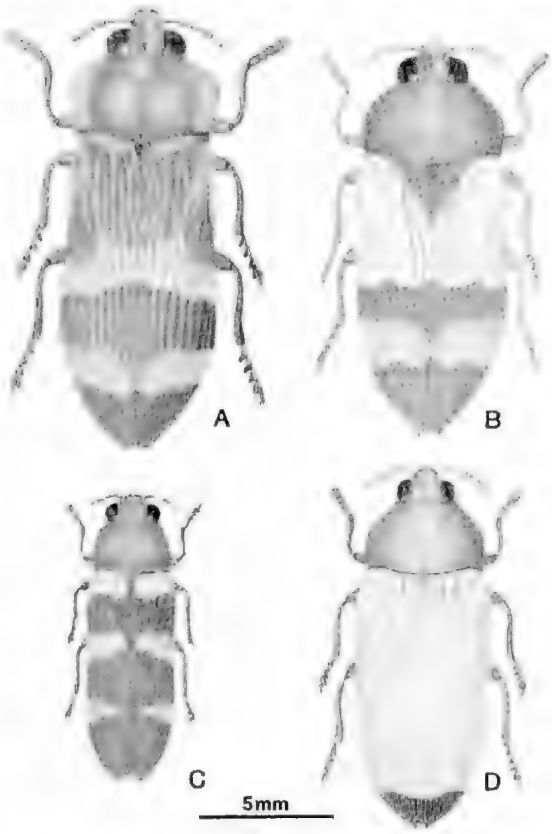

Fig. 4. Habitus illustrations of the following *Castiarina* species: A. *C. xystra* sp.nov. holotype; B. *C. chrysothoracica* sp.nov. holotype; C. *C. antia* sp.nov. allotype; D. *C. metasma* sp.nov. holotype.

Garnet, 19.i.1989, S. Lamond, MHSA; 1♂, Herberton, i.1989, S. Lamond, MHSA; 2♂♂, 1♀, Mt Garnet, 13.i.1991, R. Clarke, RCBA; 1♂, 1♀, Mt Garnet, 7.i.1992, J. Hasenpusch, JHIA; 1♂, 1♀, Mt Garnet, 9.i.1992, R. Clarke, RMNA; 1♂, 1♀, Mt Garnet, 10.i.1992, R. Clarke, RCBA; 1♂, 1♀, Mt Garnet, 10.i.1992, R. Clarke, MHSA; 1♂, Davies Creek, 18.i.1992, J. Hasenpusch, JHIA; 1♂, Kuranda, 22.i.1992, J. Hasenpusch, JHIA; 1♀, Windsor Tableland, 2.iii.1992, J. Hasenpusch, JHIA.

Colour. Head black with blue reflections. Antennae blue-green. Pronotum black medially (narrowly at apex, broadly at base) laterally red-brown. Scutellum black. Elytra reddish-brown with following markings: narrow dark blue basal margin; black sutural mark commencing medially, reaching apex expanded as black apical mark. Ventral surface and legs dark blue. Abdominal segments in some male specimens all brown. Hairs silver.

Shape and sculpture. Head closely punctured, median sulcus, muzzle short. Antennae, antennomeres: 1-3 obconic; 4-11 toothed. Pronotum shallowly punctured, deep basal fovea extending forwards to apical margin as glabrous impressed line, basal notches more marginal than medial; apical margin projecting medially, basal margin bisinuate; laterally angled outwards from base, rounded to widest part pre-medially, tapered to apex. Scutellum cordiform, few punctures, glabrous, flat. Elytra punctate-striate, intervals convex, wrinkled and punctured; laterally angled out from base, rounded at humeral callus, medially concave, rounded post-medially and narrowed to truncate spineless apex; apices diverging, apical margin subserrate. Ventral surface with shallow punctures, sparse short hair, edges of abdominal segments glabrous. S7 rounded in both sexes.

Size. Males, 16.8 ± 0.32 × 6.4 ± 0.10 mm (19). Females, 19.1 ± 0.26 × 7.6 ± 0.17 mm (10).

Male genitalia. (Fig, 1Q) Parameres slightly angled outwards from basal piece, rounded post-medially and narrowed to apex. Median lobe sharp, sides obtusely angled away. Apophysis of basal piece short, medium width, rounded apically.

Remarks. This species was confused with *C. analis* (Saunders) a smaller species occurring further south. *C. analis* has a prominent red margin around the elytra and pronotum, also their male genitalia are distinct (Fig, 1P) Name derived from *indigestus* L., confused.

Castiarina xystra sp. nov.
FIGS. 1B, 4A

Holotype. ♂, Black Mt, A.C.T., iii.1931, T. G., ANIC.

Colour. Head light blue apically, dark blue basally. Antennae blue-green. Pronotum dark blue medially, red laterally. Scutellum blue. Elytra red with following blue markings: narrow basal margin, medially expanded into large rounded mark; sinuate fascia covering humeral callus, thin red strip on each side separating last two marks; post-medial fascia expanded anteriorly and posteriorly along suture; apical mark. Ventral surface: sternum predominantly blue medially, presternum red laterally with blue spot each side close to margin, presternal process red, meso- and metasternum red medially; third coxae blue basally, red apically, abdomen predominantly red, bases of segents 5, 6, 7, 8 mainly blue. Legs blue. Hairs silver.

Shape and sculpture. Head closely punctured, median sulcus deep, muzzle short. Antennae, antennomeres: 1-3 obconic; 4-11 toothed. Pronotum closely punctured, basal fovea extending forwards to middle as impressed line, basal notches on each side more marginal than medial; apical margin projecting medially, basal margin almost straight; laterally angled outwards from base, rounded post-medially to apex. Scutellum cordiform, punctate, excavate. Elytra punctate-striate, intervals convex and punctured; laterally angled outwards from base, rounded at humeral callus,

medially concave, rounded post-medially and narrowed to spineless apex; apices hardly diverging. Ventral surface with shallow punctures, moderately hairy, hairs long on sternum, medium length on abdomen, edges of abdominal segments glabrous. S7: male truncate; female unknown.
Size. Male, 15.6 × 6.0 mm (1)
Male genitalia. (Fig. 1B) Parameres angled outwards from basal piece, rounded at apex. Median lobe sharp, sides acutely angled away. Apophysis of basal piece narrowed and rounded apically.

Remarks. The elytral pattern is similar to that found in *C. militaris* (Carter) but the basal colours differ being red in *C. xystra* and yellow in *C. militaris*. *C. xystra* is a larger species and male genitalia are different (Fig. 1A). Name derived from *xystra* L., scraper

Castiarina rayclarkei sp. nov.
FIGS 1S, 3A

Holotype. ♂, Acacia Plateau, N.S.W., 16.i.1992, R. Clarke, SAMA I 21,248.
Allotype. ♀, Acacia Plateau, N.S.W., 17.i.1992, R. Clarke, SAMA I 21,249.
Paratypes. Qld: 1 ♀, Warwick, 26.i.1992, R. Clarke, MHSA; N.S.W.: 1 ♀, Acacia Plateau, 7.ii.1992, R. Clarke, RCBA.
Colour. Head and antennae bright green. Pronotum: bright green medially and along anterior margin and base; red laterally. Elytra yellow with following black markings with green reflections: narrow mark along suture from middle to apex covering both spines. Ventral surface and legs bright green. Hairs silver.
Shape and sculpture. Head shallowly punctured, glabrous, median sulcus, muzzle medium length. Antennae, antennomeres: 1-3 obconic; 4-11 toothed. Pronotum shallowly punctured, glabrous, basal fovea; apical margin projecting medially, basal margin bisinuate; laterally parallel-sided at base, rounded medially to apex. Fovea on each side at basal angles. Scutellum scutiform, glabrous, flat. Elytra punctate-striate, intervals convex and smooth; laterally angled outwards from base, rounded at humeral callus, medially parallel-sided, rounded post-medially and narrowed to bispinose apex; small marginal spine, larger sutural spine, apices diverging. Ventral surface with shallow punctures, sparse short hair, edges of abdominal segments glabrous. S7: rounded in both sexes.
Male genitalia. (Fig. 1S) Parameres angled outwards from basal piece, rounded near apex. Median lobe sharp, sides acutely angled away. Apophysis of basal piece medium width, rounded apically.
Size. Male, 18.4 × 6.7 mm (1). Females, 20.6 × 8.0 mm (3).

Remarks. This species shows morphological similarities to *C. rollei* (Kerremans). It differs in colour, size and male genitalia (Fig. 1R) from that species. Named after Mr R. Clarke, Byron Bay.

Castiarina antia sp. nov.
FIGS 1I, 4C

Holotype. ♂, Quairading, W.A., 23.xii.1991, M. Powell & D. Knowles, SAMA I 21,250.
Allotype. ♀, 38 km N Binnu, W.A., 13.xii.1988, M. Peterson, WAMA.
Colour. Head, antennae, pronotum, scutellum ventral surface and legs purple-bronze. Elytra yellow with following dark blue markings: holotype with narrow basal margin, pre-medial fascia represented by medial spot on each elytron (allotype has broad fascia reaching margin); broad post-medial fascia reaching margin; mark covering apex. Ventral surface and legs purple-bronze. Hairs silver
Shape and sculpture. Head closely punctured, median sulcus broad, muzzle very short, hairy. Antennae compressed, antennomeres: 1-3 obconic; 4½-toothed; 5-10 toothed. Pronotum closely punctured, basal fovea extending forwards to middle as impressed line; apical margin projecting medially, basal margin bisinuate; laterally angled inwards from base, rounded to widest pre-medially, rounded to apex, laterally hairy. Scutellum scutiform, glabrous, flat. Elytra punctate-striate, intervals convex, punctured; laterally angled out from base, rounded at humeral callus, medially concave, rounded post-medially, rounded abruptly to bispinose apex; small blunt marginal spine, minute sutural spine, margin rounded and indented between spines, apices diverging; Ventral surface with shallow punctures, hairy, hairs long, edges of abdominal segments glabrous. S7: males truncate, medially indented; females rounded.
Male genitalia. (Fig. 1I) Short. Parameres parallel-sided at base, rounded outwards pre-medially, rounded to apex. Median lobe blunt, sides acutely angled away. Apophysis of basal piece narrow, rounded apically
Size. Male, 3.3 × 10.2 mm (1). Female, 3.3 × 10.7 mm (1).

Remarks. Only *Castiarina* species that has reduced number of antennomeres. The specimen illustrated is the allotype (Fig. 4C), the first specimen collected. Name derived from *antia* L., forelock.

Castiarina anthrene sp. nov.
FIG. 6E

Holotype. ♀, 7 km W Nalbarra HS (28.39S, 117.36E), W.A., 29-30.viii.1981, T. F. Houston, WAMA.
Paratype. W.A.: 1 ♀, same data as holotype, SAMA.
Colour. Head, antennae black with blue reflections. Pronotum black medially, blue laterally. Scutellum

Fig. 5. Habitus illustrations of the following *Castiarina* species: A, ♂, *luteofusca* sp.nov. holotype; B, ♂, *woodi* sp.nov. holotype; C ♂ *tenebrosa* sp.nov. holotype.

black. Elytra yellow with following black markings: narrow basal margin; pre-medial fascia not reaching margin anteriorly, extending to margin posteriorly; post-medial fascia reaching margin; apical mark, last three marks connected along suture. Ventral surface and legs dark blue. Hairs silver.

Shape and sculpture. Head closely punctured, median sulcus, very short muzzle. Antennae compressed, antennomeres: 1-3 obconic; 4½ toothed; 5-11 toothed. Pronotum closely punctured, basal fovea extending forwards to middle as glabrous line, basal notches represented by glabrous area on each side more marginal than medial, connected by glabrous posterior margin; apical margin projecting medially, basal margin almost straight; laterally parallel-sided at base, rounded to widest medially, rounded to apex. Scutellum scutiform, glabrous, excavate. Elytra costate, intervals 3, 5, 9 raised at basal half wrinkled and punctured; laterally angled out from base, rounded at humeral callus, medially concave, faintly rounded post-medially, tapered, rounded to bispinose apex; small sharp marginal and sutural spines, margin rounded and indented between, apices slightly diverging. Ventral surface with shallow punctures, moderately hairy, hairs long, edges of abdominal segments glabrous. S7: male unknown; females truncate, medially indented.
Size. Females, 11.0 × 3.6 mm (2).

Remarks. This is a very distinctive elongate species showing the typical modifications found in wasp/bee mimics. Name derived from *anthrene*, Gr., wasp.

Castiarina markhanloni sp. nov.
FIGS 1H, 6C

Holotype, ♂, Round Hill Reserve, N.S.W., 10.x.1992, T. M. S. Hanlon, SAMA I 21,251.
Allotype, ♀, same data as holotype, SAMA I 21,252.
Paratypes, N.S.W.: 13♂♂, 10♀♀, same data as holotype. MHSA.
Colour. Head, antennae, pronotum bronze-green with purple reflections. Scutellum purple. Elytra pale yellow with following dark blue markings with purple and blue reflections: narrow basal margin; pre-medial fascia ends expanded anteriorly over humeral callus and posteriorly touching margin; post-medial fascia touching margin; mark covering apex, all marks connected along suture. Ventral surface and legs purple-bronze with purple reflections. Hairs silver.
Shape and sculpture. Head closely punctured, shallow median sulcus, short muzzle. Antennae, antennomeres: 1-3 obconic; 4½ toothed; 5-11 toothed. Pronotum closely punctured, punctations small medially larger laterally, basal fovea extending forwards to middle as glabrous line then to apical margin as impressed line; apical margin projecting medially, basal margin bisinuate; laterally rounded from base, widest pre-medially, rounded to apex, laterally hairy. Scutellum small, scutiform, glabrous, flat. Elytra punctate-striate, intervals convex, wrinkled, punctured; laterally angled outwards from base, rounded at humeral callus, medially concave, rounded post-medially and narrowed to bispinose apex; small blunt marginal spine, sutural spine minute, margin in most specimens almost truncate and indented between spines, apices diverging. Ventral surface with shallow punctures, long dense hair, edges of abdominal segments glabrous. S7: truncate both sexes.
Size. Males, 9.7 ± 0.18 × 3.5 ± 0.05 mm (14). Females, 10.2 ± 0.22 × 3.9 ± 0.09 mm (11).
Male genitalia. (Fig. 1H) Short: Parameres parallel-sided from basal piece, angled outwards, pre-medially rounded then tapered, rounded at apex. Median lobe blunt, sides acutely angled away then widened. Apophysis of basal piece medium width, rounded apically.

Remarks. This species could be confused with *C. inconspicua* (Saunders). Main differences are the smaller scutellum and the strongly rounded pronotum. The male genitalia show some similarity in form

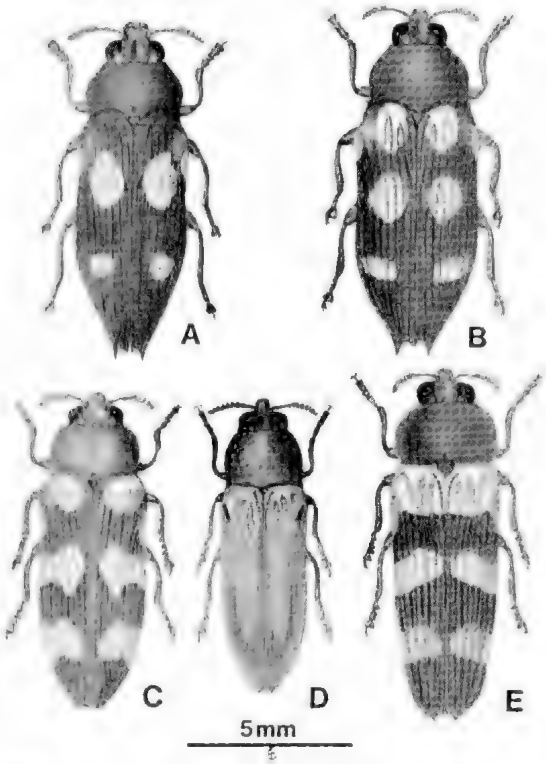

Fig. 6. Habitus illustrations of the following *Castiarina* species: A. *C. nebula* sp.nov. holotype; B. *C. hasenpuschi* sp.nov. holotype; C. *C. markhanloni* sp.nov. holotype; D. *C. mimesis* sp.nov. holotype; E. *C. anthrene* sp.nov. holotype.

although those of *C. markhanloni* are narrow and the apophysis of the basal piece is more tapered (Fig. 1G). Named after Mr T. M. S. Hanlon of Sydney.

Castiarina mimesis sp. nov.
FIGS 1F, 6D

Holotype. ♂, Badjalling, W.A., 7.xi.1970, S. Barker, SAMA I21,253.

Allotype. ♀, same data as holotype, SAMA I21,254.

Paratypes. W.A.: 15♂♂, 5♀♀, same data as holotype SAMA; 2♀♀, South Tammin Flora Reserve, 8.xi.1970, S. Barker, SAMA; 1♂, 70 km S Perth, Albany Highway, 19.xi.1970, S. Barker, SAMA; 2♂♂, 5♀♀, Northam, C. G. Jessup, SAMA; 4♀♀, no data SAMA; 1♀, 34 km N Gin Gin, 11.xi.1990, M. Powell, MPWA.

Colour. Head, antennae, pronotum bright green. Scutellum blue-green. Elytra orange with following blue markings: narrow basal margin; vitta on each elytron from humeral callus to pre-apex; line along suture meeting vittae at pre-apex. In some specimens vittae shortened at basal end leaving narrow mark over each humeral callus. Ventral surface and legs bright green. Hairs silver.

Shape and sculpture. Head closely punctured, medium sulcus, muzzle short. Antennae, antennomeres: 1-3 obconic; 4½ toothed; 5-11 toothed. Pronotum closely punctured, basal fovea extending forwards to apical margin as impressed line; apical margin projecting medially, basal margin almost straight; laterally parallel-sided from base, rounded post-medially to apex. Scutellum scutiform, glabrous, excavate. Elytra punctate-striate, intervals convex, heavily punctured; laterally angled outwards from base, rounded at humeral callus, medially concave, rounded post-medially and tapered to bispinose apex; very small marginal and sutural spines, margin rounded and indented between spines, apices hardly diverging. Ventral surface with shallow punctures, hairy, hairs long, edges of abdominal segments glabrous. S7: truncate both sexes.

Size. Males, 8.9 ± 0.19 × 2.8 ± 0.07 mm (19). Females, 8.9 ± 0.21 × 2.9 ± 0.08 mm (18).

Male genitalia. Parameres angled outwards from basal piece, rounded post-medially then increasing in width, notched apically. Median lobe blunt, sides acutely angled away. Apophysis of basal piece broad, rounded apically.

Remarks. This species was confused with *C. sanguinolenta* (C & G). Their elytral colour and markings are very similar but male genitalia are very different (Fig. 1E) and they are easily distinguished by differences in structure of their elytral spines. In *C. sanguinolenta* these are sharp and equal, in *C. mimesis* they are small and sutural spines are indented. They occur together and are part of a Muellerian mimicry complex. The name is derived from *mimesis* L., imitation.

Castiarina tenebrosa sp. nov.
FIGS 1K, 5C

Holotype. ♂, 4 km W Paluma, Qld, 7.i.1986, E. E. Adams, SAMA I 21,255.

Allotype. ♀, 4 km W Paluma, Qld, 4.i.1986, A. Sundholm, SAMA I 21,256.

Paratypes. Qld: 2♀♀, same data as holotype, ANIC; 1♂, 1♀, same data as allotype, ASSA; 2, ♂♂, 4 km W Paluma, 6/7.i.1986, A. Sundholm, ASSA.

Colour. Head, antennae and pronotum black with green reflections. Scutellum green. Elytra yellow with black markings coalesced forming basal, pre-medial and sub-apical spots, first two coalesced to form vitta also spot on humeral callus covering margin. Ventral surface green with yellow reflections. Legs dark blue. Hairs silver.

Shape and sculpture. Head shallowly punctured, broad median sulcus, short muzzle. Antennae, antennomeres: 1-3 obconic; 4½-toothed; 5-11 toothed. Pronotum shallowly punctured, small basal fovea; apical margin straight, basal margin bisinuate; laterally parallel-sided

at base, rounded to widest pre-medially, narrowed to apex. Scutellum cordiform, glabrous, flat. Elytra punctate-striate, intervals convex, punctured; laterally angled outwards from base, rounded at humeral callus, medially concave, rounded post-medially and narrowed to bispinose apex; sharp marginal spine, small, sharp sutural spine, margin straight between spines, apices diverging. Ventral surface with shallow punctures, moderately hairy, hairs medium length, edges of abdominal segments glabrous. S7: rounded in both sexes.

Size. Males, 11.9 ± 0.12 × 4.2 ± 0.06 mm (6). Females, 11.6 × 4.4 mm (2)

Male genitalia. (Fig. 1K) Parameres angled outwards from basal piece, rounded post-medially, parallel-sided, rounded to apex. Median lobe sharp, sides obtusely angled away. Basal piece wide, rounded apically.

Remarks. This species was confused with *C. guttifera* (Obenberger) which has only been collected at Kuranda, Qld. The male genitalia differ (Fig. 1J) Name derived from *tenebrosus* L., dark.

Castiarina hasenpuschi sp. nov.
FIGS 1L, 6B

Holotype. ♂, Mt Lewis, Qld, 6.i.1991, J. Hasenpusch. SAMA I 21,257.

Allotype. ♀, same data as holotype. SAMA I 21,258.

Paratypes, Qld: 1♂, 2♀♀, same data as holotype, JHIQ.

Colour. Head black with blue reflections. Antennae black with blue-green reflections. Pronotum black with purple reflections. Scutellum blue. Elytra yellow with following black markings: two fasciae and apical mark coalesced leaving a pre-medial, post-medial and pre-apical yellow spot on each elytron and one on margin at humeral callus. Ventral surface green. Legs blue. Hairs silver.

Shape and sculpture. Head closely punctured, median sulcus, short muzzle. Antennae, antennomeres: 1-4 obconic; 5-11 toothed. Pronotum closely punctured, narrow basal fovea; apical margin projecting medially, basal margin bisinuate; laterally rounded from base, widest pre-medially, rounded and narrowed to apex. Scutellum cordiform, punctured, flat. Elytra punctate-striate, intervals convex, punctured; laterally angled out from base, rounded at humeral callus, medially concave, rounded post-medially and narrowed to bispinose apex; sharp marginal spine, small, sharp sutural spine, margin straight between spines, apices diverging. Ventral surface with shallow punctures, moderately hairy, hairs short, edges of abdominal segments glabrous.

Males: legs 2 and 3 with reduced pulvilli on tarsomeres 1-3, replaced with single median spine. S7: male truncate, indented medially; female truncate, slightly indented medially.

Size. Males, 9.8 × 3.8 mm (2). Females, 10.4 × 4.0 mm (3).

Male genitalia. (Fig. 1L). Parameres short and wedge-shaped. Median lobe sharp, sides obtusely angled away. Apophysis of basal piece medium width, rounded apically.

Remarks. Structurally this species closest to members of *C. sexplagiata* group except that elytra are smooth whereas they are roughened with punctures in most members of group. Named after Mr J. Hasenpusch, Innisfail.

Castiarina luteofusca sp. nov.
FIGS 1M, 5A

Holotype ♂, Mt Lewis, Qld, 1.i.1992, G. A. Wood, SAMA I 21,259.

Allotype, ♀, Mt Lewis, Qld, 6.i.1992, G. A. Wood, SAMA I 21,260.

Paratype, 1♂, Qld: N.Q., F. P. Dodd, ANIC.

Colour. Head green. Antennae, antennomeres: 1-4 green; 5-11 blue-green. Pronotum: bronze medially; green apically. Scutellum green. Elytra yellow with black markings coalesced leaving yellow basal and medial spots on each elytron, these coalesced forming angled vitta, round yellow apical spot and yellow mark on lateral surface of humeral callus. Ventral surface green. Legs dark blue. Hairs silver.

Shape and sculpture. Head shallowly punctured, broad median sulcus, short muzzle. Antennae, antennomeres: 1-3 obconic; 4-11 toothed. Pronotum shallowly punctured, small basal fovea; apical margin projecting medially, basal margin bisinuate; laterally parallel-sided at base, angled inwards, rounded to apex, widest pre-medially. Scutellum scutiform, glabrous, flat. Elytra punctate-striate, intervals convex, punctured; laterally angled outwards from base, rounded at humeral callus, medially concave, rounded post-medially and tapered to bispinose apex; sharp marginal spine, smaller sharp sutural spine, margin rounded between spines. Ventral surface with shallow punctures, few short hairs, edges of abdominal segments glabrous. S7: truncate in both sexes.

Size. Male, 12.4 × 4.7 mm (1). Females, 12.7 × 4.8 mm (2).

Male genitalia (Fig. 1M). Parameres angled outwards from basal piece, rounded to apex. Median lobe pointed, sides acutely angled away. Apophysis of basal piece medium width, rounded apically.

Remarks. Largest of black and yellow *C. producta* (Saunders) group mimics and with *C. tenebrosa* and following new species, only ones that have yellow vittae on elytra. Name derived from *luteus* L., yellow and *fuscus* L., black.

Castiarina woodi sp. nov.
FIGS 1N, 5B

Holotype. ♂, Mt Lewis, Qld, 1.i.1992, G. A. Wood, SAMA I 21,261

Allotype, ♀, same data as holotype. SAMA 21,262.
Colour. Head and antennae blue-green. Pronotum green with bronze reflections. Scutellum blue-green. Elytra yellow with following dark green marks; markings coalesced to form yellow basal and medial spots also coalesced forming long vitta covering humeral callus and margin; large round pre-apical spot. Ventral surface green. Legs blue-green. Hairs silver.
Shape and sculpture. Head shallowly punctured; broad median sulcus, short muzzle. Antennae, antennomeres: 1-3 obconic; 4-11 toothed. Pronotum shallowly punctured, deep basal foveae; apical margin projecting medially, basal margin bisinuate; laterally parallel-sided at base, rounded to apex, widest pre-medially. Scutellum scutiform, glabrous, flat. Elytra punctate-striate, intervals convex, punctured; laterally angled outwards from base, rounded at humeral callus, medially concave, rounded post-medially to unispinose apex; sharp marginal spine, sutural spine represented by very small notch, margin straight between spine and notch, apices diverging. Ventral surface with shallow punctures, moderately hairy, hairs long and denser in medial strip, edges of abdominal segments glabrous. S7: truncate in both sexes.
Size. Male, 11.6 × 4.5 mm (1). Female, 11.9 × 4.5 mm (1).
Male genitalia. (Fig. 1N) Parameres more or less parallel-sided from basal piece, rounded to apex. Median lobe pointed, sides obtusely angled away. Apophysis of basal piece short, narrowed and rounded to apex.
Remarks. Elytral markings of this species are similar to those of *C. luteofusca* but distinctive male genitalia and elytral spines distinguish this species. Named after Mr G. A. Wood, Atherton.

Castiarina nebula sp. nov.
FIGS 1O, 6A

Holotype, ♂, Mt Lewis, Qld, 6.i.1991, J. Hasenpusch, SAMA I 21,263
Allotype, ♀, same data as holotype, SA MA I 21,264.
Paratypes. Qld: 2♂♂, Kuranda, 1.ii.1990, 5.ii.1990, G. A. Wood, GWAQ; 1♀, Kuranda, Qld, 2.i.1978, A. & M. Walford-Huggins, SAMA; 2♀♀, Kuranda, 5.ii.1990, J. Hasenpusch, JHIQ; 1♂, Kuranda, 1.ii.1990, G. Wood, GWAQ.
Colour. Head and antennae green. Pronotum black with blue or green reflections, Scutellum green. Elytra yellow with following black markings: fasciae and marks coalesced leaving six yellow spots, largest pre-medial, smallest post-medial and intermedial on margin at humeral callus. Ventral surface green. Legs blue. Hairs silver.
Shape and sculpture. Head shallowly punctured, median sulcus, medium length muzzle. Antennae, antennomeres: 1-3 obconic; 4½-toothed; 5-11 toothed. Pronotum shallowly punctured, very small basal foveae; apical margin straight, basal margin bisinuate; laterally angled inwards from base, then rounded from near base to apex, widest pre-medially. Scutellum scutiform, few punctures, glabrous, flat. Elytra punctate-striate, intervals convex, smooth; laterally angled outwards from base, rounded at humeral callus, medially concave, rounded post-medially and tapered to bispinose apex; sharp marginal spine, small sharp sutural spine, margin rounded and indented between spines, apices diverging. Ventral surface with shallow punctures, few short hairs, abdominal segments glabrous. S7: truncate both sexes. Males: legs 2 and 3 with each pulvillus on tarsomeres 1-3 replaced by median spine.
Size. Males, 10.9 × 3.8 mm (3). Females, 11.8 × 4.2 mm (4).
Male genitalia (Fig. 1O). Parameres widened from base, rounded at apex. Median lobe sharp, sides obtusely angled away. Apophysis of basal piece medium width, rounded at apex.
Remarks. Elytral markings of this species are similar to those of *C. octosignata* (Carter, 1919). However *C. octosignata* differs structurally as elytral spines are different shape. Male *C. octosignata* unknown. Name derived from *nebulosus* L., dark.

Themognatha gordonburnsi sp. nov.
FIGS 1U, 7

Holotype, ♂, 69 km N Galena Bridge, W.A., 29.ix.1992, M. Golding & M. Powell, WAMA.
Allotype, ♀, 100 km N Murchison River, W.A., 14.ix.1980, G. G. Burns, NMVA.
Paratypes. W.A.: 2♀♀, same data as allotype, 14.ix.1980, 17.ix.1980, G. G. Burns, NMVA; 9♂♂, same data as holotype, SAMA & MPWA.
Colour. Head and antennae black. Pronotum black with yellow lateral margins. Scutellum black. Elytra predominantly brown with yellow lateral margins and following black markings: narrow basal margin; females with faint pre-apical vitta over each humeral callus and faint markings on suture; post-medial fascia not reaching margin; spade-shaped pre-apical mark extending over apex. Ventral surface: male predominantly black pre-sternum with yellow mark on meta-sternal coxae; abdominal sclerites yellow with testaceous edges; female black with yellow mark on meta-sternal coxae and on lateral edges of all visible abdominal segments. Legs black. Hairs silver.
Shape and sculpture. Head punctured, hairy, apex medium length, Antennae, antennomeres: 1-3 obconic, 4 semi-toothed; 5-11 toothed. Pronotum punctured, apical margin projecting medially, basal margin faintly sinuous, laterally rounded from base to apex, bulbous pre-medially. Scutellum almost circular, flat, without punctures. Elytra punctate-striate, intervals convex and

Fig. 7. Habitus illustration of *Themognatha gordonburnsi* sp.nov. allotype.

smooth; laterally angled outwards from base, rounded at humeral callus, medially more or less parallel-sided, rounded post-medially to spineless apex. Ventral surface punctured, hairy. S7: truncate, medially indented in male; rounded in female.

Male genitalia. (Fig. 1U). Parameres angled outwards from basal piece, rounded at apex. Median lobe blunt, sides acutely angled away. Apophysis of basal piece medium width, rounded apically.

Size. Males, 20.6 ± 0.35 × 8.4 ± 0.13 mm (10). Females, 24.3 × 9.6 mm (3).

Remarks. Although the locality data on the holotype and allotype appear different they refer to the same area. The allotype has a narrow median yellow band on the pronotum, not reaching base or apical margin. *T. burnsi* is a spring emerging species, adults have been collected on the flowers of *Grevillea* sp. and *Bursaria spinosa*. On the basis of its structure and male genitalia, it can be grouped with *T. oleata* (Blackburn) a blue and red species which emerges in late summer and autumn and is usually associated with mallee flowers. The specimen illustrated is the allotype (Fig. 7), the first specimen collected. Named to commemorate my friend and colleague the late Mr Gordon Burns, Mornington.

A host plant of C. uptoni *(Barker)*

Although the adults of many *Castiarina* species are commonly collected, the pre-adult stages and host plants of even the commonest species are mostly unknown. *Castiarina uptoni* (Barker, 1979) was described from dead adults found inside tubular highway marker posts, north of Barrow Creek, N.T. Presumably they had been dropped into the cavities by predaceous insects that had been feeding on them, possibly asilid flies which commonly prey on buprestids (Barker & Inns 1976). Live specimens were subsequently collected in the same general area but their food plants were not recorded. Several years ago Herbert Demarz collected live specimens of *C. uptoni* on the leaves of *Dicrastylis georgei* Munir, a very low shrub growing in an interdune situation on Yanrey Station, 4-31 km south of Barradale roadhouse on the Great Northern Highway, W.A. On 10 August 1990, I visited the locality with Mr Demarz and we examined the same plants in that area, but found no adult beetles on the leaves. Many of the stems were dead and detached from the individual plants. Examination of the live part of each cut stem showed frass and when dissected, every one was found to be galleried and to contain a living beetle. Most were adult, but a proportion were newly pupated or in various stages of post-pupal metamorphosis. Of fourteen specimens dissected out, twelve were *C. uptoni* and two were *C. quadrifasciata* (Saunders, 1869). The two species belong to different species groups on basis of structure of their male genitalia, but are similar in body colour and pattern and thus form a Mullerian mimicry group. When I visited the same area on 20 August 1990, many *C. uptoni* adults were found on the leaves of the host plant as well as two specimens of *C. quadrifasciata*. As *D. georgei* does not occur in the N.T., beetles from the type locality must have another host plant which could be a second species of *Dicrastylis*, possibly *D. gilesii* F. Muell. which occurs in that area (Jessop 1981).

Acknowledgments

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ADULT AND LARVAL STAGES OF *PARAUSTROSTRONGYLUS RATTI* (NEMATODA: TRICHOSTRONGYLOIDEA) FROM *RATTUS FUSCIPES*

BY IAN BEVERIDGE & MARIE-CLAUDE DURETTE-DESSET†*

Summary

The morphology of the adult and the third and fourth larval stages of *Paraustrostrongylus ratti* from the native rodent *rattus fuscipes* is described, with particular reference to the synlophe, as well as the mechanism of attachment of the nematode to intestinal villi. The synlophe of the fourth larval stage has an oblique axis of orientation, in contrast to the frontal orientation in the adult stage, and most closely resembles the synlophe of species of *Dessetostrongylus* parasitic in dasyurid marsupials. Ontogenetic data therefore suggest that *Paraustrongylus* evolved from an ancestor resembling *Dessetostrongylus.*

KEY WORDS: Nematodes, Trichostrongyloidea, *Paraustrostrongylus,* ontogenesis, larvae, morphology, rodents.

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BEVERIDGE, I. & DURETTE-DESSET, M.-C. (1993) Adult and larval stages of *Paraustrostrongylus ratti* (Nematoda: Trichostrongyloidea) from *Rattus fuscipes*, *Trans. R. Soc. S. Aust.* 117(1), 27-36 4 June, 1993.

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KEY WORDS: Nematodes, Trichostrongyloidea, *Paraustrostrongylus*, ontogenesis, larvae, morphology, rodents.

Introduction

The trichostrongyloid nematode subfamily Herpetostrongylinae occurs in the small intestines of Australian marsupials and is one of the few trichostrongyloid groups in which there is apparently a close evolutionary parallel between hosts and parasites (Durette-Desset 1982, 1985; Humphery-Smith 1983; Beveridge 1986). Three distinct lineages have been recognised among the eight component genera in marsupials, each sharing a probable common ancestry with *Woolleya*, a contemporary genus which occurs in dasyurid marsupials. *Woolleya* shares features in common with the genus *Viannaia*, belonging to the family Viannaiidae, which is present in South American marsupials and rodents (Humphery-Smith 1983).

Two of the herpetostrongyline genera, *Austrostrongylus* and *Paraustrostrongylus*, occurring in diprotodont marsupials, with one species in the marsupial mole, *Notoryctes typhlops*, and one in a rodent, *Rattus fuscipes*, are of particular morphological interest due to the development of paired lateral cuticular inflations, unique within the Trichostrongyloidea, termed "floats" by Durette-Desset (1979). The evolutionary development of these floats was investigated in *Austrostrongylus* and in a related genus, *Sutarostrongylus*, (Beveridge & Durette-Desset 1986) and species with intermediate or primitive morphological features, that is either with a single float or without floats, were identified. This study suggested that *Sutarostrongylus*, parasitic in *Thylogale* spp., exhibited a number of primitive characters, ancestral to those seen in *Austrostrongylus*, but provided no additional insights into the possible relationships between a postulated *Woolleya*-like ancestor and *Sutarostrongylus*. *Dessetostrongylus* is one possible intermediary between *Woolleya* and *Sutarostrongylus* (see Beveridge & Durette-Desset 1986) as it has a synlophe, or complement of body ridges, identical with that of *Sutarostrongylus* except for the fact that the axis of orientation of the synlophe is oblique in *Dessetostrongylus* but frontal in *Sutarostrongylus*. Humphery-Smith (1983) by contrast, placed greater emphasis on the frontal orientation of the synlophe of *Austrostrongylus* and derived it directly from an ancestral state resembling that found in *Woolleya sprenti*.

Cassone *et al.* (1986), studying new species of *Woolleya* and *Patricialina* from dasyurid marsupials confirmed the direct *Woolleya* - *Austrostrongylus* relationship identified by Humphery-Smith (1983), but considered that *Dessetostrongylus* was a sister group to *Austrostrongylus*.

All studies on the evolution of the Herpetostrongylinae to date have relied on the comparative morphology of the adult nematodes and particularly on differences in the anatomy and orientation of the synlophe. The ontogenesis of larval stages is an important source of phylogenetic information in the Trichostrongyloidea (Durette-Desset 1985), but has not been exploited in the case of the Herpetostrongylinae other than in the case of *Beveridgiella pearsoni* (see Humphrey-Smith 1980), because no life cycles are known.

We decided to investigate the morphology of the various life-cycle stages of *Paraustrostrongylus ratti*, the only member of the genus to occur in a eutherian mammal (Obendorf 1979) to attempt to obtain additional information on the evolution of the synlophe of the genus. Due to its abundance in *Rattus fuscipes* and the ease with which infected rats could be obtained and kept in the laboratory, *P. ratti* was considered to

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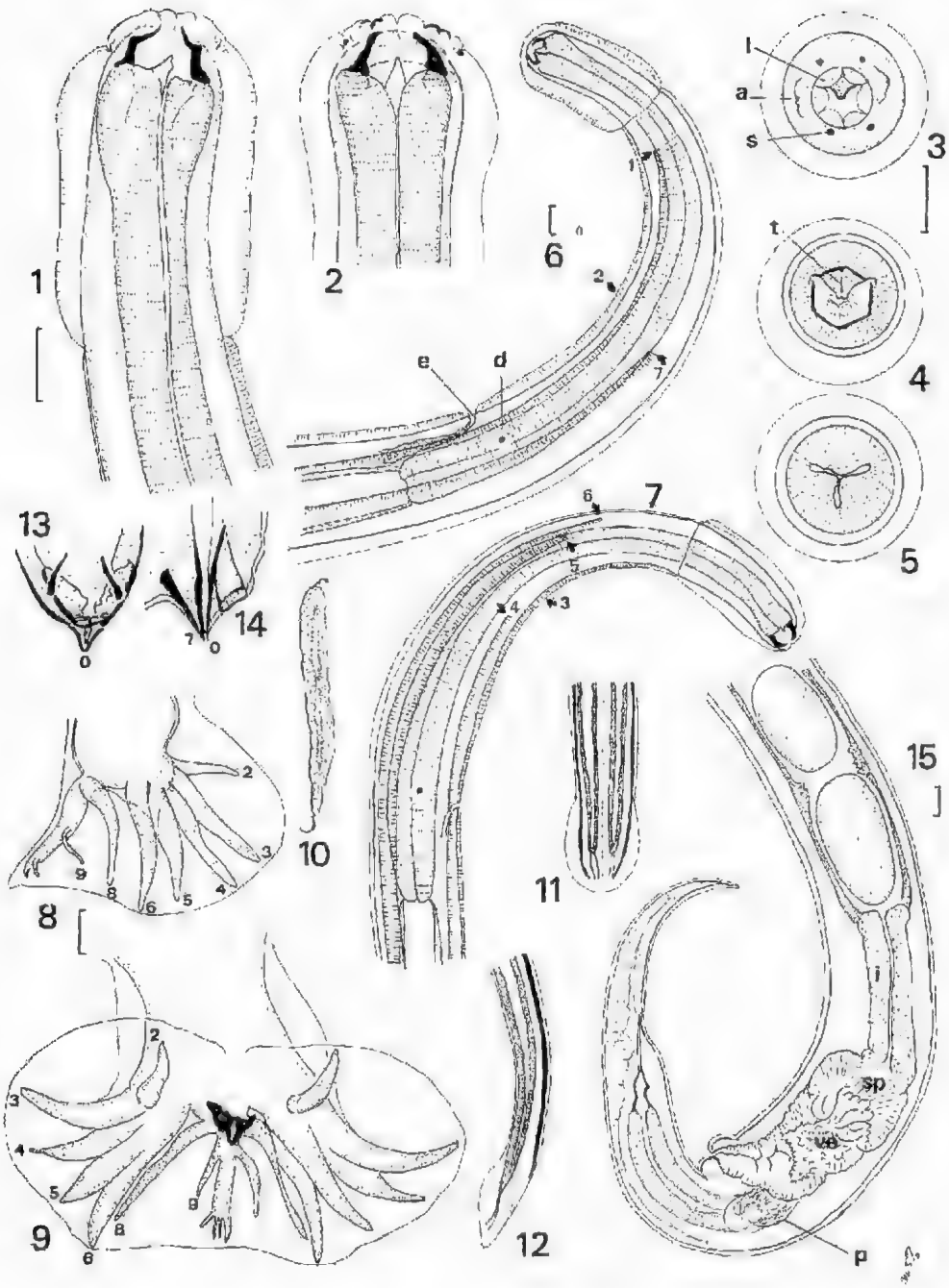


Figs 1-15. *Paraustrostrongylus ratti* Obendorf: Adult. 1, anterior end, lateral view, dorsal aspect on left hand side; 2, anterior end, dorsal view; 3, apical view of mouth opening and lips; 4 optical transverse section through hexagonal buccal capsule, with dorsal tooth; 5, transverse optical section through anterior end of oesophagus; 6, anterior region, left lateral view; arrows indicate origins of ridges; 7, anterior region, right lateral view; arrows indicate origins of ridges; 8, bursa, lateral view; numerals indicate ray numbers according to Durette-Desset (1983); 9, bursa, ventral view; 10, gubernaculum, lateral view; 11, spicule tips, ventral view; 12, spicule tip, lateral view; 13, genital cone, ventral view of papilla 0; 14, genital cone, lateral view showing papillae 0 and 7; 15, female tail, lateral view. Scale lines 0.01 mm: figs 1,2, 10, 11-14 to same scale; figs 3-5 to same scale; figs 6,7 to same scale; figs 8,9 to same scale. Legend: a, amphid; d, deirid; e, excretory pore; l, lip; p, posterior atrophic uterus; s, submedian papilla; sp, sphincter; t, dorsal tooth; ve, vestibule.

be more suitable for investigation than species occurring in marsupials. The morphological data presented here also provide the basis for subsequent ultrastructral studies.

Methods

Naturally infected rats, *Rattus fuscipes* (Waterhouse), were trapped at Blackwood, Victoria (37°29′S, 144°19′E), killed in the laboratory and the small intestine was divided into segments and opened in warm 0.09% saline. The intestinal segments were placed in an incubator for two hours to allow nematodes to migrate into the saline. Nematodes were then washed in saline and fixed in hot 70% ethanol. Small numbers of nematodes were fixed in 2.5% glutaraldehyde in phosphate buffer at 4°C.

Adult, fourth and parasitic third-stage nematodes were cleared in lactophenol and examined, using Nomarski interference contrast microscopy. Transverse sections of the body of male and female nematodes were cut using a cataract scalpel, mounted in lactophenol for examination and oriented using the methods of Durette-Desset (1971). Apical views of the anterior extremity were made by similar means. Specimens fixed in glutaraldehyde were embedded in resin. Sections cut at a thickness of 1 μm were stained with toluidine blue and were used to confirm morphological features seen in hand-cut section. Additional specimens were dehydrated in a graded ethanol series, dried in a critical point drier, coated with gold and examined with a Siemens Autoscan scanning electron microscope.

Ridges of the synlophe were numbered in an anticlockwise fashion beginning with the left-ventral ridge, in order to demonstrate homologies between stages. The numbering system for the bursal rays and papillae follows that of Durette-Desset (1985).

Faeces from naturally infected rats were collected, mixed with an equal quantity of charcoal and cultured on moist filter paper in Petri dishes at laboratory temperature. Five and eight days later, larvae emerging from the faecal-charcoal mixture were collected in distilled water and concentrated by sedimentation.

Third-stage larvae were examined live in water as well as after having been immobilised by heating. Some larvae were killed in hot 70% ethanol and cleared in glycerol by transferring to a mixture of 70% ethanol and glycerol and allowing the ethanol to evaporate.

Measurements were made either with an ocular micrometer or from drawings made using a drawing tube and are presented in the text in millimetres as the range followed by the mean in parentheses.

Morphological terminology for the synlophe follows that of Durette-Desset (1985). All drawings are oriented with the dorsal aspect uppermost and the left hand side of the nematode body towards the left margin of the page.

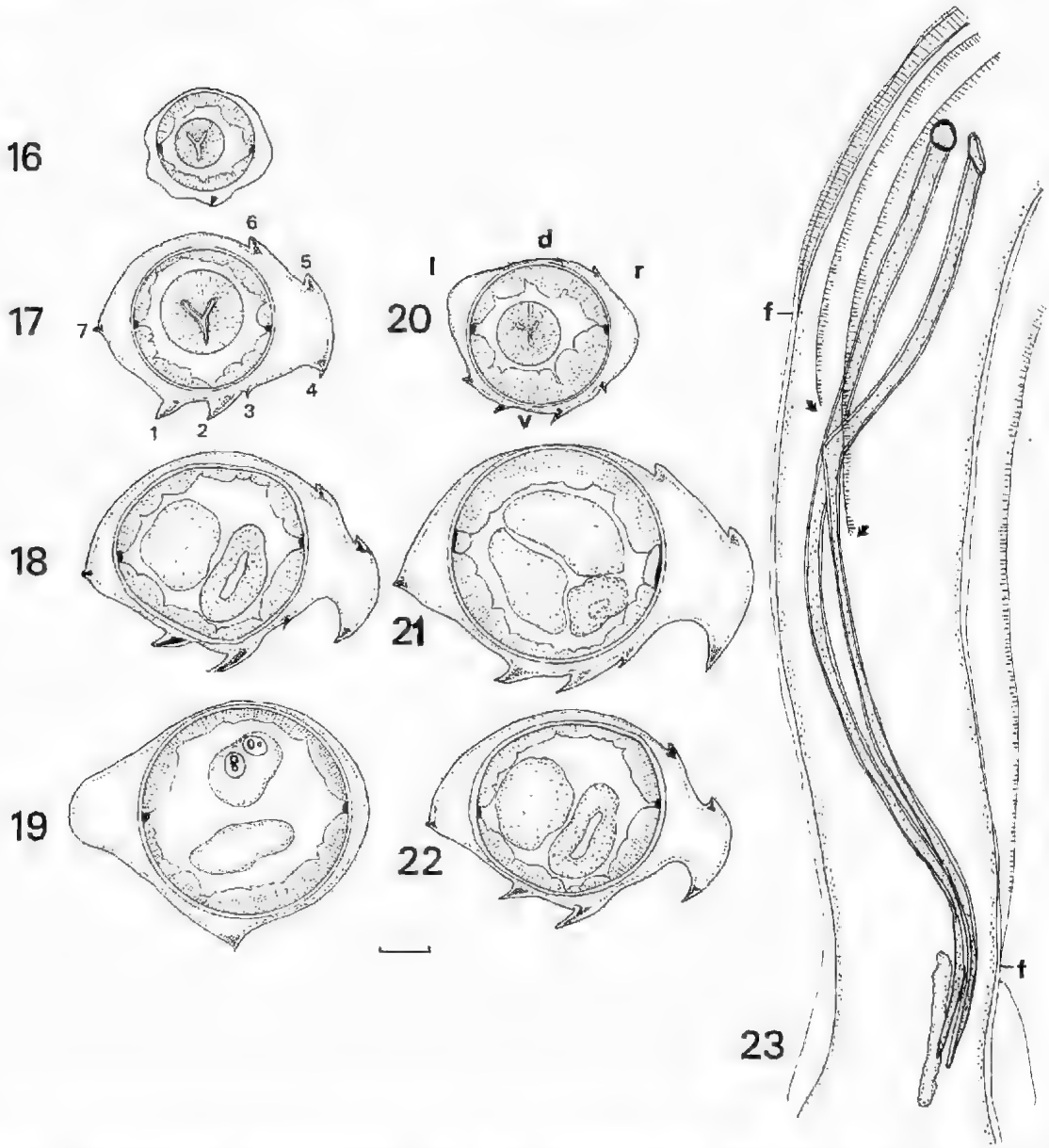
Parasitic third-stage larvae of *P. ratti* were distinguished from the synhospitalic nematodes *Nippostrongylus magnus* and *Odilia bainae* by features of the tail and cephalic extremity, based on material obtained from monospecific experimental infections with each of these two species. To obtain a monospecific infection of adult *P. ratti*, one naturally infected *R. fuscipes* was killed, all *P. ratti* in the small intestine were sorted while being maintained in warm saline, and were transferred by enterotomy to a laboratory-reared *R. fuscipes* under general anaesthesia. Four weeks later, the recipient rat was killed, the intestine removed and 10% buffered formal saline injected rapidly into it to fix nematodes *in situ*. Fragments of intestine with worms attached subsequently were dissected and prepared for scanning electron microscopy as described above. Additional segments were dehydrated, embedded in paraffin, serially sectioned at a thickness of 10 μm, and the sections stained with haematoxylin and eosin for histological examination.

Results

Adult male and female nematodes, fourth-stage larvae and two parasitic third-stage larvae were examined morphologically under the light microscope, as well as third-stage larvae cultured from faeces. Light microscopic observations were compared with scanning electron micrographs of the adults.

Parauustrostrongylus ratti Obendorf, 1979
FIGS 1-38

Description: Adult: small nematodes, red when live, spirally coiled in 3-5 tight coils, ventral surface innermost, capable of uncoiling and becoming straight when maintained in warm isotonic solutions. Cephalic extremity with prominent cephalic vesicle, 20-30 fine transverse ridges on vesicle (Fig. 1). Mouth opening, surrounded by four sub-median papillae and two amphids; no labial papillae visible; six rounded lips project into mouth opening. Buccal capsule prominently developed, heavily sclerotised, circular to sub-hexagonal in transverse section (Fig. 4), walls, arched inwards, increase in thickness towards base, lumen increases in diameter towards base; prominent tooth projects inwards from dorsal lobe of oesophagus; sub-ventral teeth absent. Oesophagus elongate, slender, clavate, widened at anterior extremity; excretory pore variable in position, usually anterior, occasionally posterior, to oesophago-intestinal junction; deirid tiny, domed, at level of excretory pore; nerve ring in mid-oesophageal region, visible in few specimens only.



Figs 16-23. *Paraustrostrongylus ratti* Obendorf: adult. 16-22, transverse sections of body. 16-19, male, 2.3 mm long; 16, at posterior end of cephalic vesicle, 0.06 from anterior extremity; 17, in oesophageal region, 0.30 mm from anterior extremity; 18, in posterior half of body, 1.60 mm from anterior extremity; 19 in cloacal region, 0.10 mm from posterior extremity; 20-22, female, 2.6 mm long; 20, oesophageal region; 21, 0.50 from anterior extremity; 22, 1.90 mm from anterior extremity; 23, posterior end of male, ventral view, showing termination of ventral ridges (arrows) and termination of floats (f). Legend: d, dorsal; l, left; r, right; v, ventral; ridges are numbered (1-7) in an anticlockwise direction from the left ventral ridge. Scale line: 0.01 mm.

Body covered with numerous fine transverse annulations (Fig. 36); two lateral, fluid-filled cavities (= floats) present on either side of body, extend from immediately posterior to vesicle to posterior region of nematode. Synlophe composed of three ventral ridges (1-3) (Fig. 36), oriented from right to left, diminishing in size from left to right; right float with two dorsal (5,6) (Fig. 35) and single ventral (4) ridge directed towards left dorsal; ridges 1-3 commence posterior to vesicle; left float, with single ridge (7) (Fig. 35) directed perpendicular to body, commences posterior to mid-oesophagus; right float with two dorsal (5,6) and one ventral (4) ridge; ridge 6 commences posterior to vesicle, followed by 5 then 4 in mid-oesophageal region.

Male (measurements of 10 specimens). Total length 1.98-2.66 (2.30); maximum width (without floats) 0.050-0.070 (0.057); cephalic vesicle 0.055-0.065 (0.064) long; oesophagus 0.27-0.30 (0.28) long, nerve ring *circa* 0.15 from anterior extremity; excretory pore 0.21-0.29 (0.25) from anterior extremity; deirid 0.22-0.30 (0.26) from anterior extremity; spicules 0.23-0.32 (0.27) long; gubernaculum 0.025-0.045 (0.037) long. Synlophe: ventral ridges and right float terminate near anterior extremity of spicules; left float continues to level of gubernaculum. Bursa symmetrical, lobes indistinct, dorsal lobe not separated from lateral lobes; rays 2 to 6 of bursa grouped in pattern of 3-2 (*sensu* Durette-Desset 1983) or 1-2-2 allowing for highly divergent ray 2; ray 2 slender, short, divergent, not reaching margin of bursa; rays 3 to 5 more robust, directed postero-laterally, of approximately equivalent size, not quite reaching margin of bursa; ray 6 shares common origin with ray 5, robust, blunt, directed posteriorly, reaches margin of bursa; dorsal trunk separate from lateral trunk; ray 8 arises from dorsal trunk, slender, does not reach margin of bursa; rays 9 slightly asymmetrical, short, slender, arise close to origin of ray 10; ray 10 stout, divides near extremity into 4 branches; outer pair of branches more robust; final branches do not reach margin of bursa. Spicules simple, elongate, alate; anterior extremities irregularly knobbed, distal tips jouted; each spicule with fine, spiniform ventro-lateral branch arising in distal 1/6-1/7 of spicule; spicule tips surrounded by expanded sclerotised flange in dorso-ventral view; each main branch of spicule terminates in two fine spiniform projections within flange; gubernaculum elongate, rectangular in dorso-ventral view, composed of two layers; genital cone heavily sclerotised, complex, conical in shape, c. 0.020 long, base 0.020 wide; papilla 0 at tip of ventral lip of genital cone; paired papillae 7 on dorsal lip of cone.

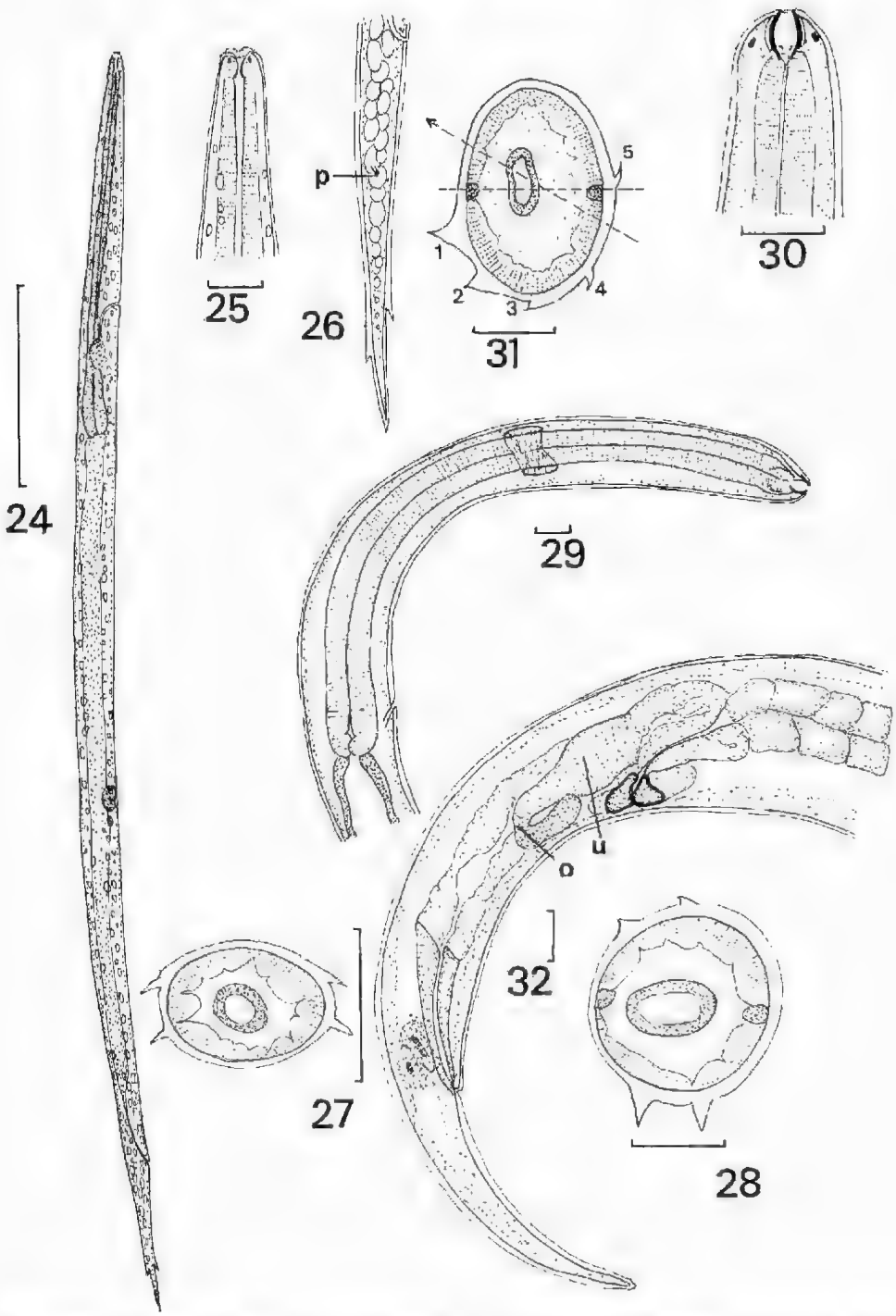
Female: (measurements of 10 specimens). Total length 2.48-2.95 (2.70); maximum width (without floats) 0.060-0.070 (0.066), with floats *circa* 0.10; cephalic vesicle 0.060-0.070 (0.063) long, oesophagus 0.26-0.32 (0.29) long; nerve ring *circa* 0.18 from anterior extremity; excretory pore 0.21-0.27 (0.23) from anterior extremity; deirid 0.22-0.26 (0.24) from anterior extremity; tail 0.08-0.11 (0.10) long; vulva to posterior extremity 0.14-0.21 (0.17); egg 0.065-0.080 (0.074) by 0.035-0.045 (0.038). Synlophe: ventral ridges extend to vulva; floats disappear in region of uterus, approx. 0.44 from tail. Tail extremely long, conical; vulva immediately anterior to uterus, opening to exterior on slight prominence; female genital system monodelphic though with posterior uterus patent and ovary persisting in vestigial form; vagina, vestibule and sphincter *circa* 0.06 long; infundibulum short, *circa* 0.04 long, prodelphic, leads to elongate uterus containing 1-4 eggs; eggs thin-shelled, ellipsoidal.

Fourth stage larva: Small nematodes, spirally coiled in 3-4 coils, ventral surface innermost; cephalic vesicle absent; mouth opening surrounded by four submedian papillae and two amphids; lips absent. Buccal capsule sub-cylindrical, heavily sclerotised; teeth absent. Oesophagus elongate, clavate; nerve ring in mid-oesophageal region; excretory pore in region of oesophago-intestinal junction. Synlophe: body floats absent; five ridges; three ventral ridges (1-3), oriented from right to left, diminishing in size from left to right; ventral ridge (4) on right hand side, oriented from right to left; single dorsal ridge (5) on right hand side, oriented dorsal from right to left; orientation of synlophe oblique from right ventral to left dorsal at about 60° to sagittal axis. Tail elongate, conical.

Male (measurements of five specimens). Total length 1.09-1.76 (1.44), maximum width 0.033-0.046 (0.040); oesophagus 0.21-0.28 (0.26), tail 0.049-0.085 (0.066).

Female (measurements of five specimens). Total length 1.47-2.00 (1.80), maximum width 0.030-0.052 (0.044), oesophagus 0.25-0.29 (0.27), tail 0.052-0.143 (0.082). Specimens with developed genitalia show distinct posterior uterus, recurving into short ovary (Fig. 32).

Third stage larva: *Parasitic*: Two parasitic third stage larvae were recorded, but detailed morphological comparisons were possible from one only. Small nematode, 0.76 long, spirally coiled in three coils; buccal capsule cylindrical, very lightly sclerotised; oesophagus slender, clavate, 0.18 long; excretory pore in posterior oesophageal region, 0.12 from anterior extremity; tail elongate, conical, with dorsal and ventral projection. Synlophe composed of two pairs of alae beginning on lateral aspects of body, perpendicular to body surface; towards mid-region of body, alae gradually shift in position to dorsal and ventral; in mid body region, the left ventral pair are larger with one in almost a mid-ventral position, and second ridge to



Figs 24-32. *Paraustrostrongylus ratti* Obendorf: larval stages. 24-27 third larval stage cultured *in vitro;* 24, entire larva, lateral view; 25, cephalic extremity, lateral view; 26, tail, lateral view; 27, transverse section in mid body region; 28, transverse section of parasitic third-stage larva from small intestine; 29-32, fourth-stage larva; 29, anterior end, lateral view; 30, buccal capsule, lateral view; 31, transverse section of larva in mid-body region, arrow indicates orientation of synlophe; 32, tail of female fourth stage larva with posterior branch of genital system. Scale lines: fig. 24, 0.1 mm; figs 25-32, 0.01 mm; figs 25-26 to same scale. Legend: p, phasmid; u, posterior uterus and o, ovary; ridges are numbered in an anticlockwise direction from the left-ventral ridge.

one side of it; two dorsal alae smaller, one almost dorsal in position, other to one side of it.

Free-living: (measurements of five specimens). Slender, elongate larvae, 0.50-0.55 (0.53) long, maximum width 0.016-0.021 (0.018); buccal capsule cylindrical, c. 0.005 long, 0.002 wide, continuous with sclerotised internal lining of anterior oesophagus; oesophagus slender, 0.14-0.16 (0.15) long; nerve ring 0.078-0.083 (0.082) from anterior end; excretory pore 0.086-0.099 (0.096) from anterior end; intestinal cells filled with granules, number of cells not ascertained; genital primordium ovoid, 0.008-0.013 (0.010) by 0.006-0.008 (0.007), 0.28-0.33 (0.31) from anterior extremity; tail elongate, conical, 0.065-0.089 (0.075) long, with dorsal and ventral spike close to tip; larva with four longitudinal alae, two on each side of body, in lateral position, almost perpendicular to body wall.

Attachment to the intestinal mucosa

Adult nematodes are coiled ventrally around intestinal villi (Figs 33, 37) usually with the tail near the distal tip of the villus; when fixed, the coils of the body are maintained (Fig. 34). At the site of attachment, nematodes compress the villi (Figs 37, 38) and, although they generally retract from the site of attachment when fixed, the impressions of the ventral ridges remain in the intestinal epithelium (Fig. 38). Changes in the epithelium at the site of attachment include cuboidal to squamous epithelial cells, elongation (= flattening) of nuclei associated with the change to a squamous cell type, loss of cytoplasmic differentiation and the loss of the brush border of microvilli. Although sometimely squamous, no defects were detected in the epithelium. No marked inflammatory changes were detected but there were significant numbers of mononuclear cells, macrophages and lymphocytes, present in the lamina propria together with a small number of eosinophils.

Discussion

Morphology of the adult

The description of the adult provided here supplements the original description by Obendorf (1979), which was found to be accurate in all essentials. Obendorf (1979) however, did not provide an apical view of the anterior extremity and provided only a single, unoriented drawing of the synlophe of the adult. In the present examination, the synlophe is described in detail, including the origins and terminations of the body ridges. Durette-Desset (1979) and Beveridge & Durette-Desset (1986) have shown that the number of body ridges changes in the posterior region of the body in several species of *Austrostrongylus* and *Paraustrostrongylus*, but comparable data were lacking for *P. ratti*. This study demonstrated that in *P. ratti*, the principal ridges arise in the oesophageal region and persist to the level of the spicules in the male and to the level of the vulva in the female. In the male, the left, but not the right float extends almost to the level of the bursa, as it does also in *P. trichosuri* and in *A. safestatus*, the latter being a species which possesses only one float. *P. ratti* also resembles *A. safestatus* in having three rather than the four ventral longitudinal ridges present in most other members of these genera.

The three principal ventral ridges arise close to the cephalic vesicle, while the ridges on the floats arise somewhat more posteriorly, with the ridge on the left float arising mid-way between the vesicle and the excretory pore and the two dorsal ridges on the right float arise in the anterior oesophageal region. The ventral ridge arises midway between the cephalic vesicle and the excretory pore. The origins and terminations of ridges have been reported in few confamilial species, but have been shown to be of considerable taxonomic use at the species level in genera such as *Nematodirus* (see Lichtenfels & Pilitt 1983). Preliminary observations by Beveridge & Durette-Desset (1986) on species of *Austrostrongylus* suggest that this may be the case in the Herpetostrongylinae, but features have been described in too few species to allow any firm conclusions to be drawn.

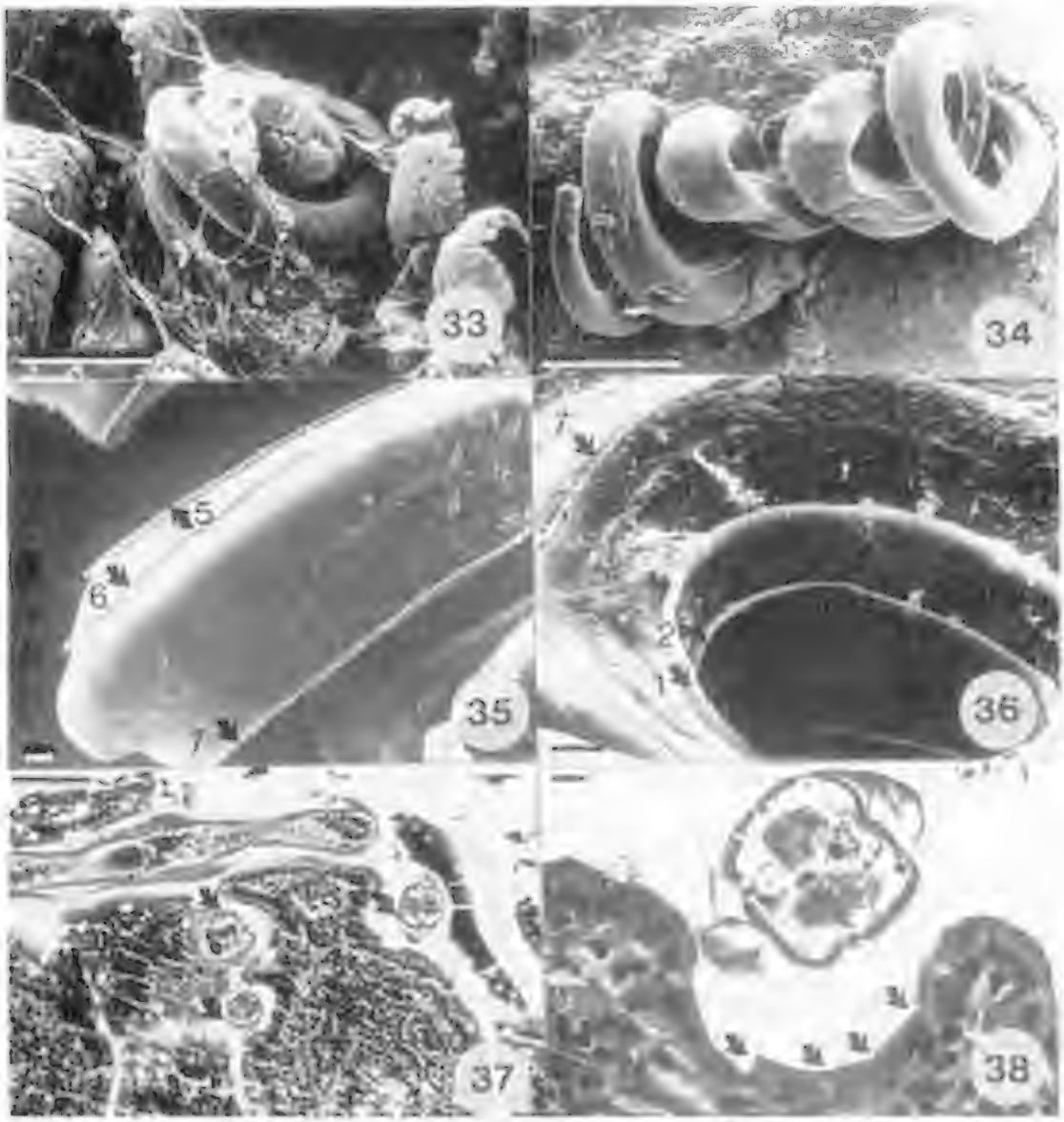
An interesting feature of the morphology of *P. ratti*, noted by Obendorf (1979) was the presence of a vestigial posterior branch to the female genital system. His observations were confirmed in this study, and the same structure was also seen in the fourth larval stage. The genera *Austrostrongylus* and *Paraustrostrongylus* are considered to be very closely related but can be separated on the basis of the presence of a sclerotised genital cone in *Paraustrostrongylus*, the absence of ventral teeth in *Paraustrostrongylus* and the position of ray 2 (Beveridge & Durette-Desset 1986). Species of *Paraustrostrongylus* are invariably monodelphic while most species of *Austrostrongylus* are didelphic. The evolution of monodelphy has occurred repeatedly in the Trichostrongyloidea (see Durette-Desset 1985) and the vestigial posterior uterus in *P. ratti* provides an obvious connection between the monodelphic and didelphic forms seen in these two closely related genera. In other trichostrongyloid genera such as *Neoheligmonella*, the posterior uterine branch may persist in the adult nematode, but does so only as a small collection of cells, posterior to the vulva (Durette-Desset & Cassone 1987), rather than the almost fully formed but diminutive posterior branch seen in *P. ratti*.

Attachment to villi

Results presented here indicate that *P. ratti* attaches to intestinal villi by coiling spirally around them, as in certain other trichostrongyloid nematodes (Durette-Desset 1985). The ventral body ridges clearly press into the intestinal epithelium, and may therefore assist

the nematode in maintaining its attachment to the villus. The ventral surfaces of both body floats are also in close apposition to the epithelium and effectively increase the surface area of the nematode in contact with the intestinal epithelium. The ventral ridge of the right float (4) and to some extent the latero-dorsal ridge (4) of the right float (5) also cause indentation of the epithelium, and may therefore also assist in attachment.

Once in place on a villus, dorsal ridges would seem to have little function in attachment, and one of the features of *P. ratti* is that it has few dorsal ridges. However, when observed in warm isotonic solutions, the nematode is capable of uncoiling completely, and evidence from the localisation of experimentally transplanted nematodes indicates that they are capable of migration within the intestine as is the case with



Figs 33-38. *Parastrongyloides ratti* Oberdorf. 33-36, scanning electron micrographs. 33, entire nematode coiled spirally around villus in small intestine; 34, entire nematode, ♀, showing body cuticle (4); anterior end to left. 35, dorsal surface of nematode showing ridges 5 and 6 of dorsal aspect of right body float and ridge 7 on lateral aspect of left float. 36, ventral surface of posterior region of body showing ridge 7 on left body float and ventral ridges 1 and 2. 37, longitudinal section through villus showing posterior part of nematode coiled around villus, with anterior end extending to left of field; 38, histological section through villus at point of attachment of *P. ratti*, with nematode retracted, showing sites of indentation (arrows) of ridges in epithelium. Scale bars: figs 33, 34, 37, 0.1 mm; figs 35, 36, 38 0.01 mm.

other trichostrongyloids (see Croll & Ma 1977). The dorsal ridges may therefore be of use during nematode migrations within the small intestine, when they are uncoiled and are moving between villi.

Morphology of Larval stages

The morphology of the buccal capsule of the fourth stage of *P. ratti* resembles very closely that of the fourth stage of *B. pearsoni* (see Humphery-Smith 1980) in peramelid marsupials and *Globocephaloides trifidospicularis* (see Beveridge 1979), a species parasitic in macropodid marsupials. The Globocephaloidinae, to which the latter genus belongs, was placed within the Herpetostrongylidae by Durette-Desset (1983) based on features of the bursa and buccal capsule. Since members of the sub-family lack a synlophe, their precise affinities have not been established. However, the similarities between the fourth stage larvae of *G. trifidospicularis*, *B. pearsoni* and *P. ratti* provide additional evidence that the two subfamilies are related.

Only two parasitic third larval stages of *P. ratti* were found. However, they were identified by the characteristics of the tail, which was identical to that of larvae cultured from faeces. Both parasitic larvae were spirally coiled, as are the fourth stage and adult. The pairs of alae which were clearly lateral in position at the anterior and posterior extremities of the body were slightly shifted in position in the mid-body region so that the larger, left pair were almost ventral in position, while the smaller, right pair became almost dorsal in position. This gradual shift in ridge position and the hypertrophy and ventral shift of one pair of alae presumably aids in attachment, as is the case in the adult. Two pairs of lateral alae were evident in the free-living third larval stage but they remained in the lateral position throughout the length of the nematode body. Several other trichostrongyloids have paired lateral alae in the third stage larva (Eckert & Schwarz 1965; Durette-Desset & Cassone 1987). The apparent change in orientation of the ridges in the mid-body region during the initial parasitic phase of the life cycle appears to assist the nematode in attaching to villi, but the mechanism by which this might occur is unclear. Usually there is no change in the synlophe unless a moult occurs, but in this instance, the change in position of the alae is visible in the entire nematode as well as in sections. Additional observations are clearly needed to confirm the results reported here.

Evolutionary relationships

The description of the fourth larval stage of *P. ratti* provides additional insight into the evolution of the Herpetostrongylidae. The type of information which can be provided by the larval synlophe has been discussed by Durette-Desset (1985). Generally, the larval synlophe demonstrates primitive features compared with that of the corresponding adult and frequently resembles the adults of other, related genera thereby allowing phylogenetic reconstructions. In the case of *P. ratti*, as in other trichostrongyloids, the larval synlophe differs markedly from that of the adult. The larva lacks floats; in the larva, the axis of orientation is oblique rather than being frontal, as occurs in the adult and the synlophe has two fewer ridges, lacking those found on the left float and on the dorsal right float of the adult. The larval synlophe of *P. ratti* most closely resembles that found in the adults of *Sutarostrongylus* and *Dessetostrongylus* but differs from that of *Sutarostrongylus* in having one rather than two dorsal ridges, and in orientation since the synlophe of *Sutarostrongylus* has a frontal orientation, similar to that of the adult *P. ratti*. The oblique orientation of the synlophe of the larval stage of *P. ratti* resembles that of *Dessetostrongylus*, from which it differs only in having fewer dorsal ridges. The homology of ridges between adult and larva here considered to be most likely is that ridges 1 to 3 of the larva correspond with ridges 1 to 3 of the adult, while the two additional ridges of the larva (4 and 5) correspond to two of the ridges on the right float of the adult (4 and 5). An alternative possibility would be that the first four ridges from left to right correspond to the four ventral ridges present in most species of *Austrostrongylus* and some species of *Paraustrostrongylus*, with the fifth ridge corresponding to one of the ridges on the right float. This interpretation involves postulating the loss of a ventral ridge in adult *P. ratti* and the appearance of two rather than one new ridge for the right float. The more parsimonious of the two hypotheses has been chosen here. It is also consistent with the hypothesis of Humphery-Smith (1983) that species of *Woolleya* with three left-ventral, obliquely oriented ridges, were the likely ancestors of *Dessetostrongylus*.

The suggested intermediate forms in the proposed transition series for the evolutionary lineage between *Woolleya* and *Austrostrongylus/Paraustrostrongylus* have been *Beveridgiella* (see Durette-Desset 1982; Humphery-Smith 1983) and *Dessetostrongylus* (see Beveridge & Durette-Desset 1986). *Patricialina*, an additional possibility, has a frontally symmetrical synlophe, while both *Beveridgiella* and *Dessetostrongylus* have an oblique orientation to the synlophe. *Patricialina* was considered to have been derived from *Beveridgiella* by Humphery-Smith (1983) and Cassone *et al* (1986). *Beveridgiella* has a greater number of dorsal ridges than *Dessetostrongylus*, and increases in the number of ridges occur in a number of evolutionary lineages within the Trichostrongyloidea (Durette-Desset 1985), suggesting that the synlophe in species of *Beveridgiella* is probably derived from a *Dessetostrongylus*-like ancestor. This in fact is shown in the larval stage of *B. pearsoni* (see Humphery-Smith

1980), which has a synlophe close to that of *Dessetostrongylus*. The synlophe of the fourth-stage larva of *P. ratti* differs from that of adult *Dessetostrongylus moorhousei* only in lacking an extra dorsal ridge. Because of the close correspondence between their synlophes, it appears likely that *Paraustrostrongylus* evolved from an ancestor resembling contemporary species of *Dessetostrongylus*, thus supporting the hypothesis proposed by Beveridge & Durette-Desset (1986) and Cassone *et al.* (1986).

Acknowledgments

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A NEW SPECIES OF *GRILLOTIA* AND *PSEUDOGRILLOTIA* (CESTODA: TRYPANORHYNCHA) FROM AUSTRALIAN SHARKS, AND DEFINITION OF THE FAMILY GRILLOTIIDAE DOLLFUS, 1969

BY R. A. CAMPBELL* & I. BEVERIDGE†

Summary

Two new species of trypanorhynch cestodes *Grillotia amblyrhynchos* sp. nov. and *Pseudogrillotia spratti* sp. nov., are described from the spiral valves of carcharhinid sharks in Australian waters. *G. amblyrhynchos* is distinguished from congeners by possessing seven hooks per principal row, four intercalary hooks that merge with a wide longitudinal band of small hooks on the external tentacular surface, and a basal armature with microhooks on the external surface. *Pseudogrillotia spratti* sp. nov. is the fourth species in the genus and differs from congeners in the absence of a basal swelling, lack of a pars post-bulbosa, 9-10 hooks per principal row, absence of a band of hooks from all but the basal region of the tentacle and a single row of intercalary hooks. The subfamily Grillotiinae Dollfus, 1942 and the family Pseudogrillotiidae Dollfus, 1969 are discussed. The subgenus *Paragrillotia* and family Pseudogrillotiidae are rejected. Grillotiidae Dollfus, 1969 is formally defined for the first time and the three genera, *Grillotia* Guiart, 1927, *Progrillotia* Dollfus, 1969 and *Pseudogrillotia* Dollfus, 1969 are admitted with revised diagnoses.

KEY WORDS: *Grillotia, Pseudogrillotia,* cestode, new species, Australia.

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KEY WORDS. *Grillotia*, *Pseudogrillotia*, cestode, new species, Australia.

Introduction

Few records of *Grillotia* or its relatives exist from studies of the cestode parasites of Australian fishes. Three *Grillotia* species have been described from larvae taken from Australian teleosts, one by Shahsrom & Lester (1982) and two by Sakanari (1989). The genus *Pseudogrillotia* was not listed as occurring in the Australian region in a checklist of the parasites of fishes by Beumer *et al.* (1982). A new species of *Pseudogrillotia* from a carcharinid shark reported herein therefore constitutes the first record of this taxon in the Australian region and a new species of *Grillotia* represents the first description of an adult of this genus from the region.

Materials and Methods

Cestode specimens were fixed in 10% formalin and transferred to 70% ethanol for storage. Tentacles were dissected free and mounted in glycerine jelly or balsam to facilitate examination. Whole mounted cestodes were stained with Celestine Blue, dehydrated in a graded ethanol series, cleared in clove oil and mounted in Canada Balsam. Terminology and numbering of tentacular hooks follows Dollfus (1942).

Measurements are given in micrometers as the range followed by the mean in parentheses, unless otherwise indicated. The number of measurements is indicated as (n). All specimens were measured. Type specimens have been deposited in the South Australian Museum, Adelaide (SAM).

Drawings were made with a drawing attachment on an Olympus BH microscope. In the figures, vitelline follicles are shown only along the lateral margins of proglottides for the sake of clarity.

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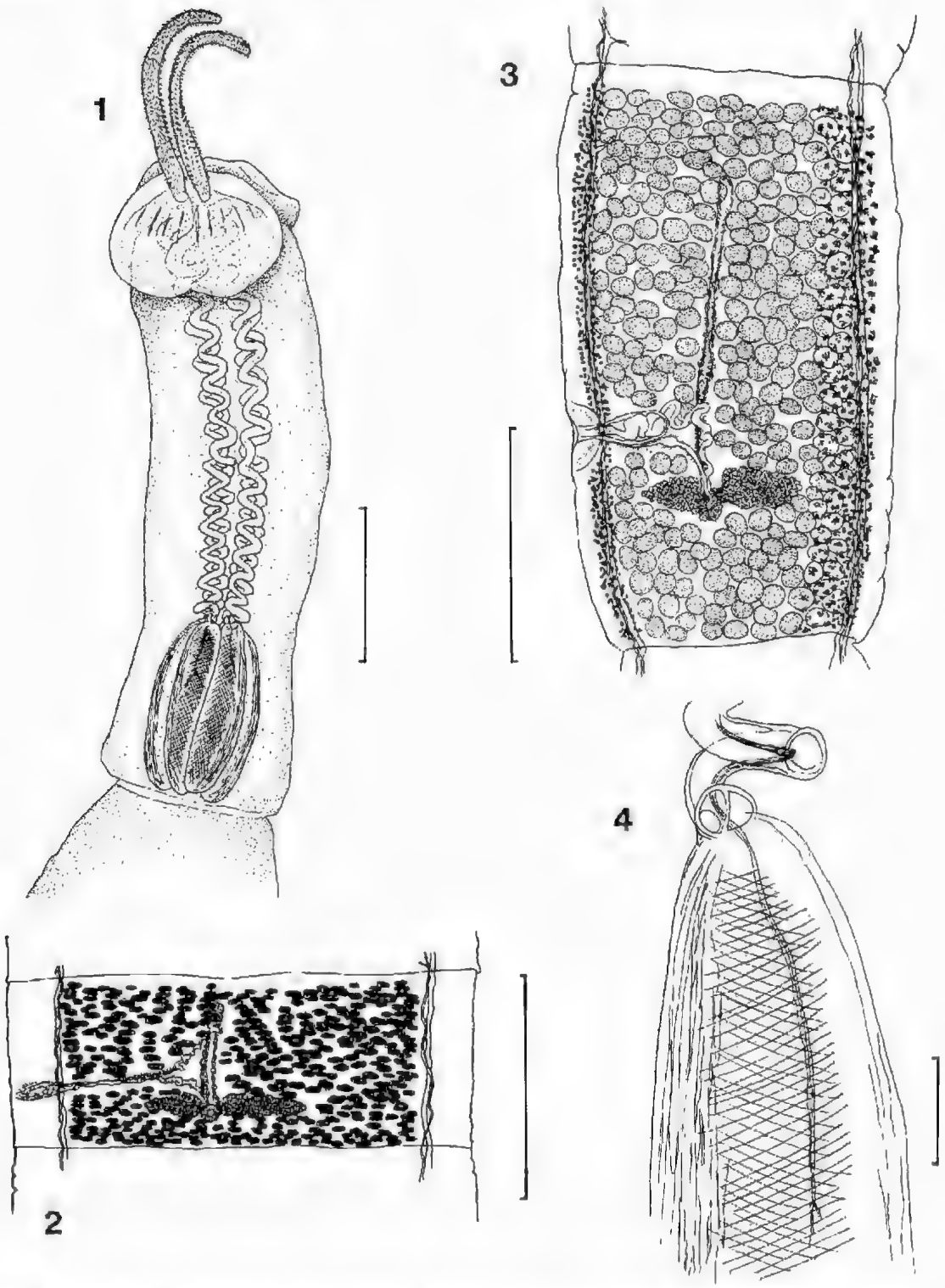
Grillotia amblyrhynchos sp. nov.
FIGS 1-9

Types: Holotype: from spiral valve of *Carcharhinus amblyrhynchos* (Bleeker, 1856), Townsville, Queensland, 4.xii.1985, coll. B. G. Robertson, SAM V4213; paratype: 1 specimen, same date, SAM HC23332.

Description: Moderate sized worms, total length up to 30 mm. Scolex (n=2) long and broad, 3.9, 4.2 mm long, 1.18 mm wide at level of bulbs. Two broadly oval, patelliform bothridia, 710-900 (780) long by 1070-1180 (1120) wide, notched on posterior border, margins only slightly thickened and curved medially, posterior and lateral borders free; adherent surface spinose with a narrow median fissure c. 266 long, paralleled by four smaller fissures on either side at regular intervals (Fig. 1). Pars vaginalis 2.56, 2.74 mm long. Tentacle sheaths spiral; prebulbar organs distinct. Bulbs 1140-1180 long by 232-264 in diameter; retractor muscle originates at midlength of bulb. Pars post-bulbosa lacking. Ratio of pars bulbosa to pars vaginalis 1:2.3



Figs 1-4. *Grillotia amblyrhynchos* sp. nov.; 1, scolex; 2, immature proglottis showing testes; 3, mature proglottis, vitellaria shown only at margins; 4, bulb and prebulbar organs. Scale lines: 1-3, 1 mm; 4, 0.1 mm.

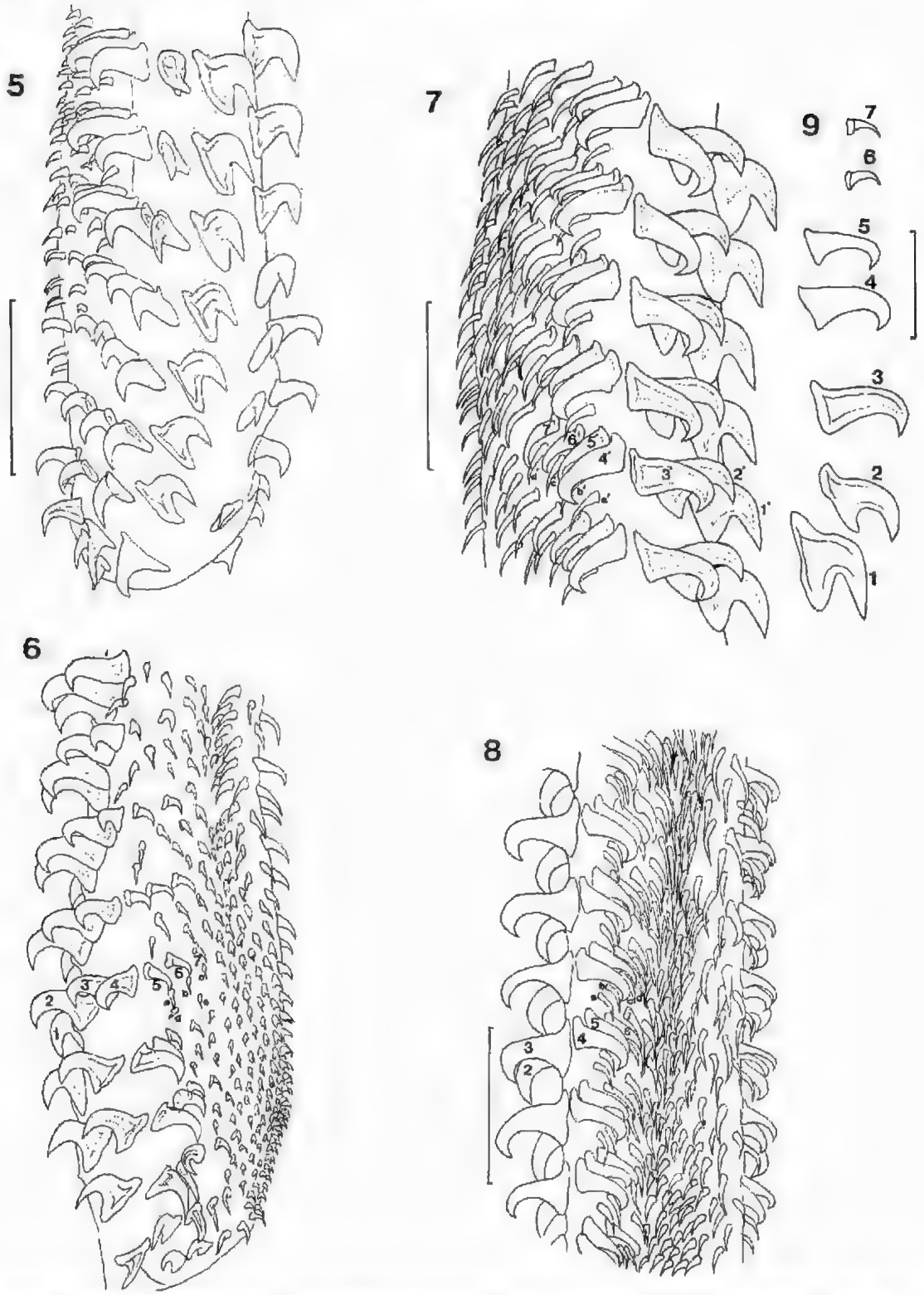
to 1:2.4. Scolex ratio (pbo:pv:phulb) 1:3.3:1.4. Tentacles short, length 1.40-1.46 mm, tapering, tending to collapse; diameter at base 110-144, diameter at mid-tentacle 95, diameter at tip 34. Armature heteroacanthous (*sensu* Beveridge & Campbell 1989), heteromorphous, with band of small hooks in metabasal region; hooks hollow. Basal armature consists of numerous microhooks on external face between first four principal rows of hooks (Fig. 6); internal face of basal armature consists of large hooks, reduced in size from those of metabasal region. Principal hook rows alternate, consist of ascending half-spirals of seven hooks each; rows begin on internal surface, merge with band of small hooks on external surface of tentacle (Fig. 8). Hooks of first proximal row (base of tentacle) reduced in size and number; hooks 1(1′) of first proximal row well separated but with transverse bases. Hooks 1(1′) in all other rows, separated by distinct space, bases oriented longitudinally, rose-thorn shaped, gradually increasing to maximum size at mid-tentacle then decreasing in size toward tip of tentacle, length 36-63 (52), base 34-46 (41), with distinct heel 4-11 (9) and toe 4-13 (10), height 23-38 (32) (n=10). Hooks 2(2′) rose-thorn shaped, similar to 1(1′) but smaller, length 36-49 (42), base 27-38 (31), heel 8, toe 9, height 19-29 (23). Hooks 3 (3′) erect, falciform, with extended heel 4-6 (5), toe absent, hook length 34-44 (39), base 19-23 (22), height 22-30 (27). Hooks 4(4′) and 5(5′) falciform, erect slightly smaller, heel reduced, toe lacking; 4(4′) length 29-42 (38), base 10-15 (13), heel 4, height 17-23 (24); 5(5′) length 23-25 (24), base 11, heel 2, height 17-24 (20). Hooks 6(6′) and 7(7′) spiniform, smaller in proximal rows 1-4, length 10-15, but with distinct toe 4-6; toe absent from these hooks distal to row 4; 6(6′) length 17-21 (19), base 10, height 11-19 (15); 7(7′) length 15-21 (16), base 8-10 (9), height 13-18 (16). Hooks 6(6′) and 7(7′) of principal rows much reduced and merge with band of hooks on external surface of tentacle. Viewed from bothridial or antibothridial surfaces of metabasal region, single row of 3-4 intercalating hooks between principal rows beginning with hooks 4(4′) or 5(5′). Second intercalary row of two hooks may be present between principal rows in basal region of tentacle. Intercalary hooks spiniform, length 11-19 (15), base 5-6 (5), height 6-16 (10). Intercalary hook rows merge with irregularly arranged band of hooks on external surface. Band of hooks opposite proximal rows 1-10 small, uncinate, length 8-13 (10), base 4-6 (5), height 4, toe 4. Remainder of hooks forming band distal to row 10 spiniform, length 11-21 (18), base 4-8 (6), toe absent, heel 2, height 11-19 (17).

First evidence of segmentation about 680 from scolex, segments narrow, gradually increasing in length with maturity, becoming twice as long as wide when mature. Mature segments acraspedote, 1.92-2.36 mm (2.22 mm) by 1.40-1.50 mm (1.45 mm), terminal segments c. 2.50 mm by 1.44 mm. Genital pores lateral, irregularly alternate, post-equatorial, 60-64 percent of segment length from anterior margin in mature segments. Cirrus (or possibly an hermaphroditic) sac pyriform, 258-400 by 133-140, containing sinuous sperm duct. No armature visible. External seminal vesicle not observed. Testes subspherical, 200 by 180, numerous, about 376-532 (420) in mature segments, occupying all available space medial to osmoregulatory canals including postovarian space. Vagina narrow, surrounded by gland cells, closely parallels posterior border of cirrus sac, forming a bulbous dilatation ventral to proximal pole of cirrus sac, then turns posteriorly at midline as dilated tube and extends to ovarian isthmus to form narrow fertilization duct. Ovary 144-176 by 656-728, subterminal, consisting of two small, transversely elongated asymmetrical lobes joined by short isthmus, poral lobe smaller, lobes subdivided into numerous lobules. Mehlis' gland immediately posterior to ovarian isthmus, c. 144 in diameter. Vitellarium follicular, forming layer encircling osmoregulatory canals and reproductive organs. Uterus simple, median tube, terminating in anterior one-fifth of segment. Ventral osmoregulatory canal largest, diameter 38; dorsal osmoregulatory canal extremely narrow, sinuous, diameter 2.

Etymology: The species is named after its host, *C. amblyrhynchos*.

Remarks: Presently, there are 20 valid species of *Grillotia* (see Sakanari 1989).

G. amblyrhynchos sp. nov. has characters of the subgenus *Paragrillotia* which Dollfus (1969a) created to accommodate species of *Grillotia* in which the band of hooks could not be distinguished from the adjacent intercalary rows (i.e. the intercalary rows merged with the band of hooks). Only two species have been attributed to the subgenus *Paragrillotia*, *G. (Paragrillotia) simmonsi* Dollfus, 1969 and *G. (Paragrillotia) rowei* Campbell, 1977. Caira & Gavarrino (1989) provided a redescription of *Rhynchobothrium simile* Linton, 1900 and showed that *G. (P.) simmonsi* Dollfus, 1969 was a junior synonym of it. They proposed the new combination *G. similis* but did not discuss Dollfus' (1969a) placement of the species, now recognized as *G. similis*, in the subgenus *Paragrillotia*. Conceptually, the creation of *Paragrillotia* as a subgroup of *Grillotia* is useful except for the fact that *G. simmonsi* does not fit the subgeneric definition. *Grillotia (P.) rowei* was the first species described that met the subgeneric definition (Campbell 1977). *G. amblyrhynchos* sp. nov. is a second species with this subgeneric character. The problem is not resolved by retaining *G. simmonsi* as type of the subgenus *Paragrillotia*. *Paragrillotia*, then, should be eliminated on the basis of its chosen type species.



Figs 5-9. *Grillotia amblyrhynchos* sp. nov.; tentacular armature: 5, basal region, internal face; 6, basal region, external face; 7, metabasal region, bothridial face; 8, metabasal region, external face; 9, hooks 1 through 7 of principal row. Scale lines: 5-8, 0.1 mm; 9, 0.05 mm.

Both *G. similis* and *G. rowei* have six hooks per principal row unlike *G. amblyrhynchos* sp. nov., which has seven hooks per principal row. None of the remaining species of *Grillotia* has seven hooks per principal row (Sakanari 1989). In *G. similis* and *G. amblyrhynchos* there are four hooks per intercalary row. There are two or three intercalary hooks per row in *G. rowei* but the hooks have transversely elongated bases whereas those of *G. amblyrhynchos* are oval and have a longitudinal orientation. In *G. similis*, the first two intercalary hooks in each row (a and b) are twice the length of intercalary hooks c and d whereas in *G. amblyrhynchos* the intercalary hooks are subequal. The group of microhooks on the external face of the basal armature of *G. amblyrhynchos* is absent in *G. similis* and *G. rowei*. The presence of microhooks in the basal armature is typical of 15 species of *Grillotia*.

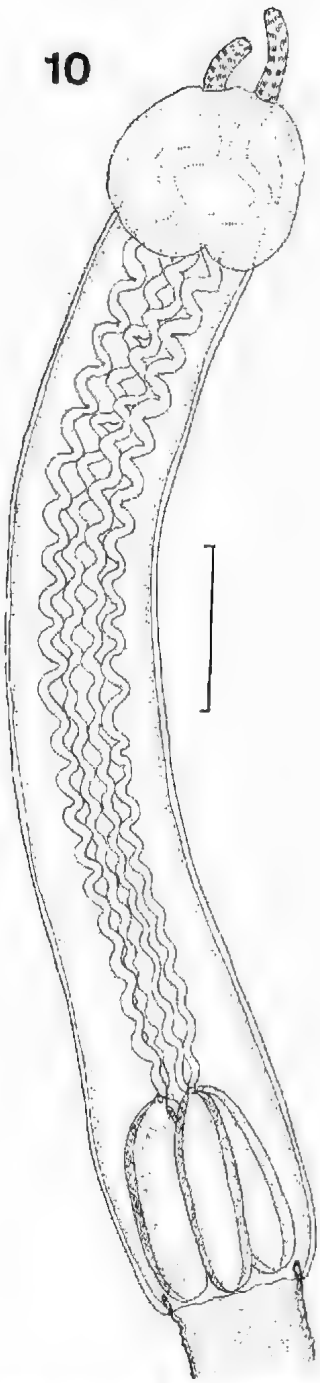
Differences in the numbers of hooks across the bands of these species is worthy of note. In *G. similis* only a single hook file remains between the intercalary rows and principal rows on the external face (See Fig. 8, Caira & Gavarrino 1989). In Fig. 19 of Dollfus (1969a) the band of hooks of *G. simmonsi* is reduced to 1-3 hooks in width if one disregards all the principal hooks and intercalary hooks. Therefore, the characteristic feature for the subgenus *Panagrillotia* of having the intercalary rows merge imperceptibly with the "band" of hooks is misleading because there is only a single file of hooks rather than a band exclusive of the intercalary and principal rows. In fact, this armature pattern demonstrates an intermediate pattern of symmetry between atypical heteroacanths and pocciloacanths with a single chainette. In *G. rowei* a single large hook and two small hooks are present on each side of the external face between the opposing principal rows and in *G. amblyrhynchos* a band 6-8 spiniform hooks in width is present. The mature proglottides of *G. similis* and *G. amblyrhynchos* possess postovarian testes, a feature Dollfus (1969b) considered significant in separating *Progrillotia* from *Grillotia*. An hermaphroditic sac was noted in *G. crimaceus* by Dollfus (1942), and this feature has been confirmed by us in additional material of the species. It was also shown to occur in *G. similis* by Caira & Gavarrino (1989). Beveridge & Campbell (1988) have pointed out the presence of an hermaphroditic sac in numerous trypanorhynchs and have remarked upon the generic and even familial significance of the genital terminalia.

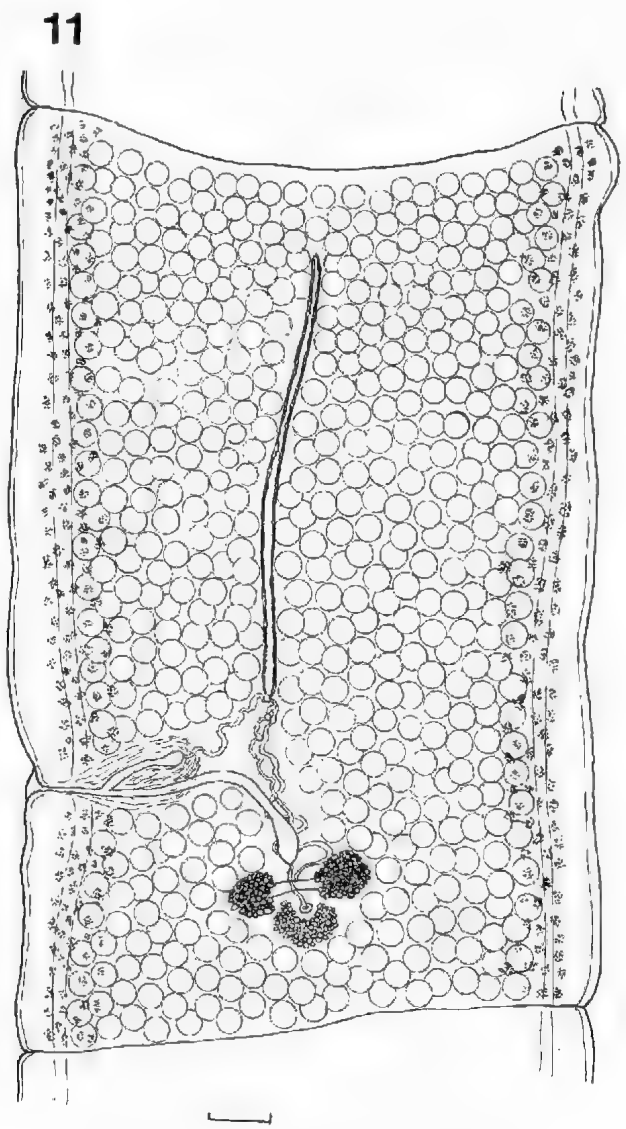
Pseudogrillotia spratti sp. nov.
FIGS 10-16

Types: Holotype: from spiral valve of *Carcharhinus brachyurus* (Guenther, 1870), Tathra, N.S.W., 31.xii.1984, coll. D. M. Spratt, SAM V4212; paratypes: four specimens, same data AHC HC23331.

Description: Scolex craspedote, very long and slender, 6.2-8.4 mm (7.4 mm; n=5) long, maximum width 0.88-1.16 mm (1.00 mm) in region of bulbs; two patelliform bothridia, 740-980 (880) wide, posterior margin indented, with a pair of fissures on lateral margins. Pars bothridialis 0.88-1.00 mm (0.95 mm); tentacle sheaths regularly sinuous; pars vaginalis 5.6-7.1 mm (6.4 mm); bulbs short and wide, 1.12-1.28 mm (1.21 mm) long by 220-340 (270) wide; prebulbar organs prominent; retractor muscle origin undetermined. Pars postbulbosa absent. Velum very short, 30-80 (50). Scolex ratio (pbl: pv: pbulb) 1: 6.7: 1.3. Tentacles up to 1.2 long, 70-140 (110) in diameter, basal swelling lacking. Armature heteroacanthous, heteromorphous; hooks hollow. Principal rows of hooks alternate, ascending in half spirals of 9-10 hooks per row from external surface. Hooks 1(1′) separated by a wide space, rose-thorn shaped, large, 70-100 (85) long, base length 60-70 (65), height 40-60 (50, n=10); hooks 2(2′) rose-thorn shaped, smaller, 60-75 (70) long, base 40-60 (45), height 55-80 (66). Hooks 3(3′) to 9(9′) elongate, slender, bases narrow, gradually diminishing in size, recurved at tip; 3(3′) length and height 65-85 (77), base 15-35 (25); 4(4′) length and height 70-90 (84), base 15-30 (23); 5(5′) length and height 65-80 (72); 6(6′) length and height 60-80 (65); 8(8′) length and height 45-80 (62); 9(9′) length and height 48-70 (62); 10(10′) length and height 44-56 (49). Single row of six intercalary hooks, 20-32 (23) long, present between principal rows aligned with principal hooks 5(5′) to 10(10′). In basal region, principal hooks of bothridial surface larger than those of antibothridial surface; ascending series of six hooks in file number 1, lengths 72, 55, 60, 70, 90, 95; hooks in file number 1′, lengths 100, 90, 85, 90, 95. Internal surface of basal armature with band of small microhooks, 12-28 (16) long, extending in closely spaced V-shaped rows along tentacle but ending at level of fifth principal rows; band of microhooks diminishes from 12 hooks wide proximally at first principal rows to four hooks distally at fifth principal rows; band of hooks absent distal to fifth principal row of hooks.

Longest specimen 50 mm, with about 65 segments; first mature segment about number 50. Segments acraspedote, largest mature segment 1.8 mm by 0.97 mm; genital pore in posterior half of segment, 80% from anterior margin; irregularly alternate. Testes numerous (>500), filling all available intervascular medullary space, forming thick postovarian band, 40-60 (50, n=10) in diameter; vas deferens visible at level of ovarian isthmus, coils extending just anterior to level of genital pore then laterally to enter cirrus sac. Hermaphroditic sac weakly developed, about 230 by 90; external seminal vesicle present, weakly developed. Vagina tubiform, diameter about 20, joining





Figs 10-11. *Pseudogrillotia spratti* sp. nov.; adult worm: 10, scolex; 11, mature segment. Scale lines: 10, 1 mm; 11, 0.1 mm.

cirrus within hermaphroditic sac to form hermaphroditic duct. Vagina curves posteriorly to ovarian isthmus, dilating to 40 but not forming distinct seminal receptacle. Ovary immature, lobes 150 by 80. Mehlis' gland posterior to ovarian isthmus, 160 by 90; uterine duct coils anteriorly nearly to level of hermaphroditic sac; uterus tubular, ascends anteriorly nearly to anterior end of segment, uterine pore absent. Vitelline follicles form a circum-medullary sleeve around proglottis. Lateral osmoregulatory canals barely visible.

Remarks: Dollfus (1969a) created the genus *Pseudogrillotia* and the family Pseudogrillotiidae for *P. pleistacantha* because of its combination of two bothridia, craspedote scolex, metabasal armature with a band of numerous small hooks, lack of a chainette and possession of a postlarval stage. Carvajal *et al.* (1976) added a second species, *P. basipunctata*, from *C. amblyrhynchos* in Hawaii. *P. spratti* sp. nov. is similar to *P. pleistacantha* in the number of hooks per principal row and lack of a basal tentacular swelling but can be distinguished from *P. pleistacantha* by (1) lack of a continuous band of small hooks in the metabasal armature and (2) lack of a pars post-bulbosa and velum. The new species can be distinguished from *P. basipunctata* by (1) the lack of a continuous band of hooks in the metabasal armature, (2) lack of a well developed basal armature, (3) absence of a basal swelling and (4) more hooks per principal row (9-10 vs. 6).

P. peruviana described by Escalante & Carvajal (1984) is most similar to *P. spratti* sp. nov. in having the band of hooks restricted to the basal region of the tentacle but is readily distinguished from the new species by (1) possession of four intercalary hook rows between each pair of principal rows compared with one intercalary row in *P. spratti*, and (2) differences in the shape of the large basal hooks (Fig. 14).

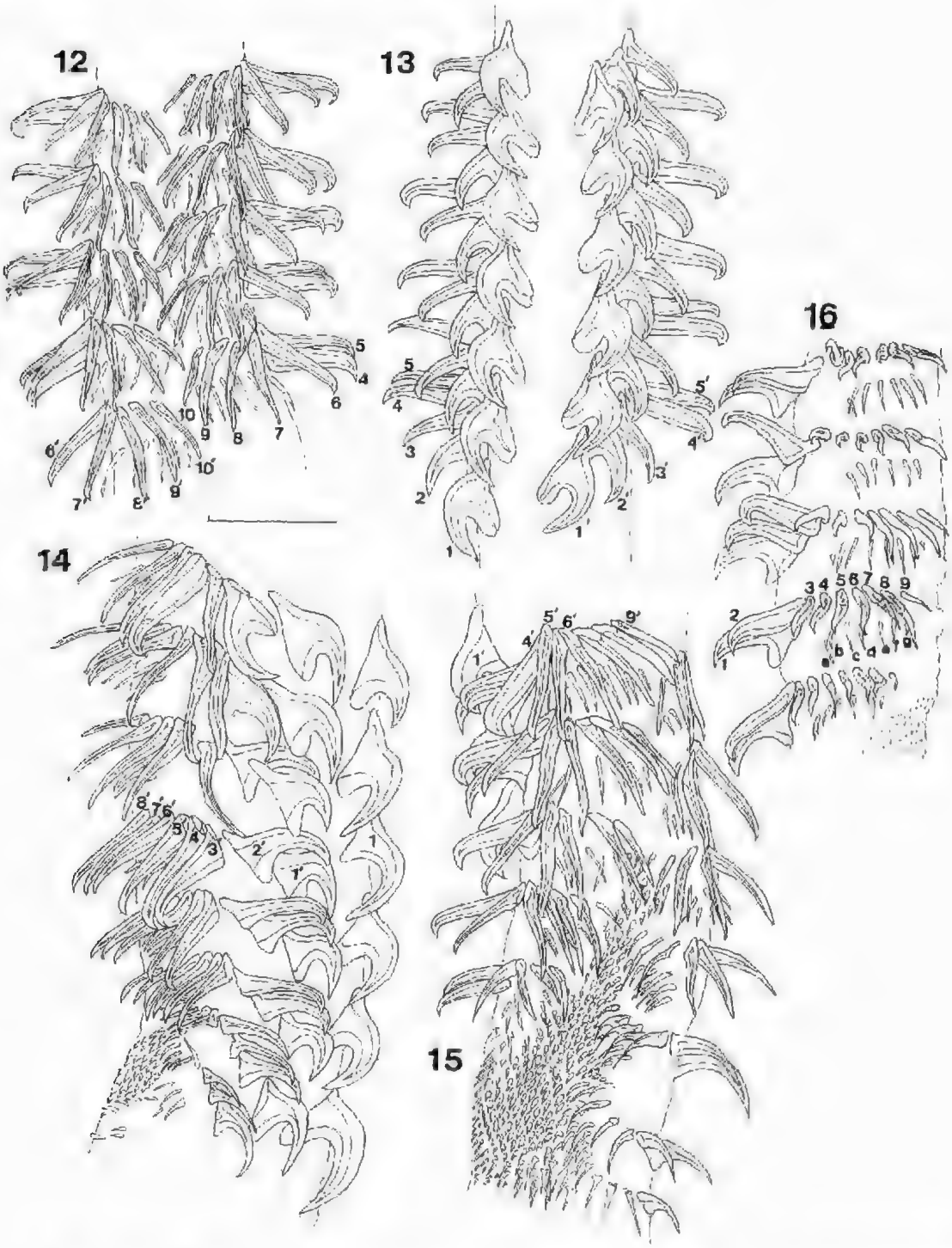
Carvajal *et al.* (1976) emended the family diagnosis of Pseudogrillotiidae with the description of the first species based upon an adult worm. The diagnosis is still in agreement with *P. spratti* and *P. peruviana* except that, as in species of Ptembothriidae, viz. *P. hawaiiensis* Carvajal Cornford & Campbell, 1976, the band of hooks may be absent from the metabasal armature. All other characters are in agreement.

Discussion

Trypanorhynch cestodes of the subfamily Grillotiinae Dollfus, 1942 and the family Pseudogrillotiidae Dollfus, 1969 have been reported from sharks and skates in the Mediterranean, North Atlantic, off the west coast of both North and South America, Hawaii and recently from Australian waters. Dollfus (1942) created the subfamily Grillotiinae within the family Lacistorhynchidae Guiart, 1927 distinguishing it from other poeciloacanths with two bothridia by (1) possession of a longitudinal band of hooks instead of a chainette and (2) presence of intercalary hooks between the principal rows. He further noted the possession of two notched patelliform bothridia, craspedote scolex and lack of a postlarval stage (without blastocyst). In a separate paper, Dollfus (1946) created the subgenus *Progrillotia* to accommodate a new species that lacked postovarian testes and later (Dollfus 1969b) elevated *Progrillotia* to generic status with an emended diagnosis, distinguished from *Grillotia* by very long bulbs, no enigmatic prebulbar organs, absence of postovarian testes and a external band of hooks that is discontinuous but merges with the interpolated rows of hooks. Dollfus (1969a) also created the subgenus *Paragrillotia*, and the family Pseudogrillotiidae.

Dollfus (1969a) emphasized the distinction between the armatures of *Grillotia* and *Lacistorhynchus* by erecting a new family Grillotiidae because it separated genera with chainettes (*Lacistorhynchus*, *Callitetrarhynchus*, *Flericeps*; *vide* Beveridge & Campbell 1989) from genera with intercalary rows and a longitudinal band of hooks on the external surface, i.e. *Grillotia*. Dollfus' (1969a) distinction stands in contradiction to the keys of Yamaguti (1959) and Schmidt (1986). We agree with Dollfus (1969a) and recognize a further distinction of the armature possessed by grillotiids as being suitably accommodated by the definition of "atypical heteroacanthous" in which "there are more rows of hooks on the external face than on the internal face (of the tentacle)". Our interpretation of trypanorhynch armatures includes the Grillotiidae, Pterobothriidae, Molicolidae, Otobothriidae and Rhinoptericolidae as atypical heteroacanths thus separating those families with intercalary rows and longitudinal "bands" of hooks from their former classical inclusion with the poeciloacanthous families possessing chainettes. In our opinion the term "poeciloacanth" is best restricted to families with chainettes, as defined by Beveridge & Campbell (1989), and considered distinct from those with longitudinal "bands". Thus, the poeciloacanthous ("chainette") families are Dasyrhynchidae, Lacistorhynchidae, Hornelliellidae, Mustelicolidae, Gymnorhynchidae, and Mixodigmatidae (see Beveridge & Campbell 1989).

Dollfus' attempts (1969a) to subdivide species of *Grillotia* have been prompted by their rather homogeneous armatures and varied combinations of other scolex features. He created the subgenera *Grillotia*, *Progrillotia*, and *Paragrillotia*. *Paragrillotia*, discussed and rejected above, remained a subgenus. *Progrillotia* Dollfus, 1946 was elevated to generic status and a new genus and family, *Pseudogrillotia*



Figs 12-16. *Pseudogrillotia spratti* sp. nov.; tentacle armature: 12, metabasal armature, external surface; 13, metabasal armature, external surface showing origin of principal rows; 14, basal region, internal surface on right side and bothridial surface at left; 15, basal region, transition between the basal armature and metabasal region on the external surface; 16, lower metabasal region, antibothridial surface showing single intercalary row of hooks. Scale lines: 12-16, 0.1 mm.

(Pseudogrillotiidae) were added by Dollfus (1969a). Schmidt (1986) included the genus *Grillotia* and *Pseudogrillotia* in his key but omitted *Progrillotia* and the family Pseudogrillotiidae. We concur with Schmidt (1986) in considering a craspedote scolex and postlarval stage insufficient to warrant separation of *Pseudogrillotia* into another family. We have found no paper in which Dollfus ever formally defined the family Grillotiidae but he did contrast the Grillotiidae as well as the subfamily Grillotiinae (Dollfus 1969a) in the justification for creating *Pseudogrillotia* and the Pseudogrillotiidae.

Despite the increasing number of species described and the variability in the combination of characters now apparent, Dollfus' treatment of the group has remained basically unchanged since 1969. The diverse combinations of characters and taxonomic importance previously attributed to them must be questioned in view of species recently described. The various combinations include patelliform versus non-patelliform bothridia, craspedote or acraspedote scolex, presence or absence of prebulbar organs, long or short bulbs, various origins of the retractor muscle, presence or absence of a postlarval stage between the blastocyst stage and adult, presence or absence of a basal armature, presence or absence of a demarcation between the intercalary hooks and the longitudinal band of hooks on the external surface, and even the interpretation of the presence of a longitudinal "band" of hooks for some species. For the reproductive system the details of the terminal genitalia are not well known but a hermaphroditic sac, combined with an accessory, external and internal seminal vesicles have been shown to occur in several species, the ovary may be terminal or subterminal in position, and postovarian testes are present in some species and lacking in others. As proposed by Dollfus (1942) the sub-family Grillotiinae is justified as separate from the Lacistorhynchinae in the lack of a chainette, presence of a longitudinal "band" of hooks in the metabasal armature, and presence of intercalary rows of hooks in the armature. These same characters are implied as supporting elevation to family rank (Dollfus 1969a). Complete revision of the family Grillotiidae should be made based upon examination of types of all species. The diversity of characters and combinations is not unique to *Grillotia*, but many of these same combinations can be found in the Gilquiniidae (see Beveridge 1990). We propose that they be accommodated by including them in a formal diagnosis of the family and recognised separately from the Lacistorhynchidae as follows:

Grillotiidae Dollfus, 1969 emended

Diagnosis: Scolex acraspedote or craspedote. Two wide bothridia, cordiform or patelliform, with or without thickened rims, posterior and lateral margins free. Principal hook rows alternate, intercalary rows of hooks present, irregular band of small hooks between termination of principal rows in metabasal armature. Basal armature present or absent. Hooks heteromorphous, hollow. Pars vaginalis long, tentacle sheaths sinuous. Bulbs long or short, prebulbar organs present or absent. Retractor muscle originates in posterior half or bulb. Segments acraspedote, apolytic. Mature segments elongated. Genital pores marginal, irregularly alternate. Accessory seminal vesicle, internal seminal vesicle and hermaphroditic duct present in type species. Hermaphroditic duct, external and internal seminal vesicles reported for some species. Testes medullary, some usually postovarian. Ovary usually separated from posterior segment margin by a space. Vitelline follicles form a continuous sleeve around the internal organs. Uterus saccate with lateral diverticular. Procercoid in copepods, pleroceri and postlarvae in teleosts, adults in elasmobranchs.
Type genus: *Grillotia* Guiart, 1927

Diagnosis: Grillotiidae, acraspedote scolex; bothridia indented on posterior border, longitudinal "band" of hooks continuous, intercalary rows of hooks may merge with "band", special basal armature absent, prebulbar organs present, hermaphroditic sac present, internal and external (or accessory) seminal vesicles present, ovary well forward, postovarian testes present. Other genera: *Progrillotia* Dollfus, 1969

Diagnosis. Grillotiidae, acraspedote scolex, bothridial margins not indented posteriorly, prebulbar organs lacking, longitudinal "band" of hooks interrupted opposite each principal row, special basal armature may be present, bulbs very long, prebulbar organs lacking, testes in longitudinal rows, accessory seminal vesicle absent, ovary at posterior extremity of segment, postovarian testes absent. Type species: *Pr. pastinacae* Dollfus, 1946.

Pseudogrillotia Dollfus, 1969

Diagnosis: Grillotiidae, craspedote scolex, bothridia indented posteriorly, prebulbar organs present, longitudinal "band" of hooks continuous but may be restricted to basal region; special basal armature absent, hermaphroditic duct present, testes racemose, ovary well forward of posterior margin, postvaginal testes present, postlarval stage in life cycle. Type species: *P. pleistaccentha* Dollfus, 1969.

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ABUNDANCE AND LIFE HISTORY OF NATIVE AND INTRODUCED EARTHWORMS *(ANNELIDA: MEGASCOLECIDAE* AND *LUMBRICIDAE)* IN PASTURE SOILS IN THE MOUNT LOFTY RANGES, SOUTH AUSTRALIA

BY G. H. BAKER, V. J. BARRETT*, R. GREY-GARDNER** & J. C. BUCKERFIELD***

Summary

Seasonal abundance of the native earthworm, *Gemascolex walkeri* (Megascolecidae), and introduced earthworms, *Aporrectodea rosea* and *Octolasion cyaneum* (Lumbricidae), was monitored in three pastures in the Mt Lofty Ranges, South Australia. Highest numbers of earthworms were recorded in late winter and early spring. Densities of up to 108, 32 and 96 m^{-2} were recorded for *G. walkeri, A. rosea* and *O. cyaneum* respectively. All three species of earthworms occurred predominantly in the top 10 cm of soil for four to five months per year (autumn to spring), when soils were wettest. During other seasons, they were found lower in the soil profile. Distributions within pastures were patchy and could, in some cases, be explained by soil type (*A. rosea)* and soil moisture (*G. walkeri).* Although introduced species of earthworms generally predominate in pastures in southern Australia, native species such as *G. walkeri* can occasionally constitute a substantial proportion of the total earthworm population.

KEY WORDS: Earthworms, Megascolecidae, Lumbricidae, pastures, South Australia, depth profile, life history.

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ABUNDANCE AND LIFE HISTORY OF NATIVE AND INTRODUCED EARTHWORMS (*ANNELIDA: MEGASCOLECIDAE* AND *LUMBRICIDAE*) IN PASTURE SOILS IN THE MOUNT LOFTY RANGES, SOUTH AUSTRALIA

by G. H. BAKER*, V. J. BARRETT*, R. GREY-GARDNER** & J. C. BUCKERFIELD**

Summary

BAKER, G. H., BARRETT, V. J., GREY-GARDNER, R. & BUCKERFIELD, J. C. (1993) Abundance and life history of native and introduced earthworms (Annelida : Megascolecidae and Lumbricidae) in pasture soils in the Mount Lofty Ranges, South Australia *Trans. R. Soc. S. Aust.* 117(1), 47-53, 4 June, 1993.

Seasonal abundance of the native earthworm, *Gemascolex walkeri* (Megascolecidae), and introduced earthworms, *Aporrectodea rosea* and *Octolasion cyaneum* (Lumbricidae), was monitored in three pastures in the Mt Lofty Ranges, South Australia. Highest numbers of earthworms were recorded in late winter and early spring. Densities of up to 108, 32 and 96 m^{-2} were recorded for *G. walkeri*, *A. rosea* and *O. cyaneum* respectively.

All three species of earthworms occurred predominantly in the top 10 cm of soil for four to five months per year (autumn to spring), when soils were wettest. During other seasons, they were found lower in the soil profile. Distributions within pastures were patchy and could, in some cases, be explained by soil type *(A. rosea)* and soil moisture *(G. walkeri)*.

Although introduced species of earthworms generally predominate in pastures in southern Australia, native species such as *G. walkeri* can occasionally constitute a substantial proportion of the total earthworm population.

KEY WORDS: Earthworms, Megascolecidae, Lumbricidae, pastures, South Australia, depth profile, life history.

Introduction

Australia has a rich native earthworm fauna, dominated by the Megascolecidae (Jamieson 1981). However, information on the life histories, distributions and abundances of these native species and the factors influencing them is scarce (Wood 1974; Jamieson 1981; Abbott *et al.* 1985; Baker *et al.* 1991, 1992a). The distributions of introduced species in Australia (e.g. Lumbricidae), are better understood (Abbott 1982, 1985; Abbott & Parker 1980; Tisdall 1985; Kingston & Temple-Smith 1989; Baker *et al.* 1991, 1992a), and there have been some studies of their life histories and population dynamics (Barley 1959a; Tisdall 1985; Rovira *et al.* 1987; Kingston 1989; McCredie *et al.* 1992; Baker *et al.* 1992b). The influence of earthworms, either native or introduced, on soil structure and fertility in Australia has received little study (Barley 1959b,c; Barley & Jennings 1959; Abbott & Parker 1981). Increased knowledge of the ecology and functional importance of the resident communities of earthworms in Australian soils will assist in developing improved management strategies that may lead to increased plant production and help reduce soil degradation (Baker 1989a,b).

Baker *et al.* (1992b) demonstrated the seasonal abundances and depth profiles of two introduced species, *Aporrectodea trapezoides* and *A. caliginosa* (Lumbricidae), in five permanent pastures in South Australia. *A. trapezoides* and *A. caliginosa* were active and abundant in the root zone for three to seven months, from autumn to spring, when soil moisture was highest. Mature adults were present from mid-winter to mid-spring. Patchy distributions of both species were found within some of the pastures and were partly explained by variation in soil type.

This paper reports the seasonal abundances, life histories, lateral and vertical distributions and species associations of native and introduced earthworm species that were found together with the more abundant *A. trapezoides* and *A. caliginosa* at three of the pasture sites sampled by Baker *et al.* (1992b).

Materials and Methods

Three permanent pastures in the Mt Lofty Ranges, South Australia were sampled for earthworms each month from March 1990 until November 1990 (Tungkillo) or January 1991 (Birdwood and Parawa). The climate of the region is Mediterranean, with cool moist winters and hot dry summers. Mean annual rainfall varied between sites (Tungkillo, 575 mm; Birdwood, 750 mm and Parawa, 900 mm) as did soil type (Tungkillo, uniform sand [Uc1.4]; Birdwood, yellow and black duplex soils [Dy3.4 and Dd1.1] and Parawa, yellow duplex soil [Dy2.2]) (Northcote 1979). The yellow and black duplex soils are Palexeralfs and the uniform sand is a Quartzipsamment in the US Soil Taxonomy (Soil Survey Staff 1987). Baker *et al.*

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(1992b) provide further information on chemical and physical properties of the soils at each site.

At each site, soil samples were taken within a 50 × 50 m plot that was divided into five 10 m wide strips. Each month, three random samples were taken within each strip at Tungkillo and Birdwood and two samples were taken within each strip at Parawa. Each sample was $0.1m^2$ × 30 cm deep. The samples were separated into three depths, 0-10 cm (within which the majority of plant roots occurred), 10-20 cm and 20-30 cm. The soil was hand-sorted for earthworms and cocoons which were preserved in 70% ethanol.

Approximately 400 g of soil were collected from the 0-10 cm layer in one sample from each strip for gravimetric moisture determination. These soil samples were collected every month except March 1990. Curves relating matric suctions of soil water to gravimetric water content were calculated for the soils at each of the three sites using the filter paper method (Greacen *et al.* 1989). This enabled comparisons of soil moisture availability between sites.

Species were identified within two weeks of collection, using the keys in Jamieson (1974) and Sims & Gerard (1985). Worms were separated into juveniles (no genital markings), subadults (with genital markings but no mature clitellum) and adults (with mature clitellum).

Two soil types (yellow and black duplex soils) occurred within the plot at Birdwood. The distributions of these soils were mapped by taking 25 regularly spaced auger samples (each 3 cm wide × 50 cm deep) within the plot and supplementing these with additional samples where the soil boundaries were unclear. There were no obvious spatial variations in soil type within the other two plots.

The regular sampling at Tungkillo indicated that soil moisture varied markedly within the plot, being highest near the centre and eastern edge. This pattern was possibly related to the drainage characteristics of the site, the moistest soil being found in the lowest lying areas within the plot. To check this perceived pattern in soil moisture, 22 auger samples (10 cm in diameter) were taken at random co-ordinates throughout the plot during March 1991, soil being collected from 0-10, 10-20, 20-30, 30-40 and 40-50 cm below the surface. Gravimetric soil moistures were determined for each depth.

Results

Abundance and Life History

Data for the seasonal abundance and life history of three earthworm species that were commonly collected at Tungkillo, Birdwood and Parawa are given in Figs 1 and 2. Similar data for rarer populations of these and other species found at the three sites are given in Table 1.

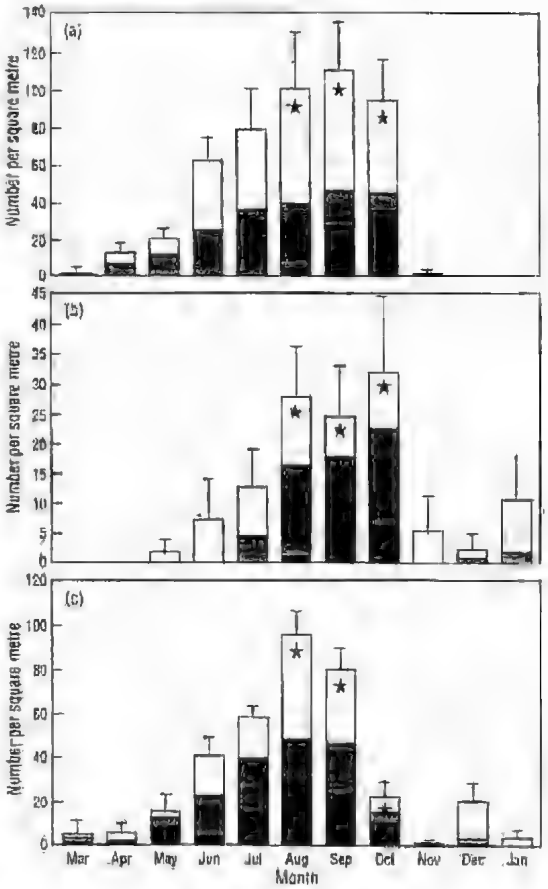

Fig. 1. Numbers (m^{-2}) of juvenile ( ), sub-adult ( ) and adult ( ) *Gemascolex walkeri* (Tungkillo) (a), *Aporrectodea rosea* (Birdwood) (b) and *Octolasion cyaneum* (Parawa) (c) collected during 1990-91. Standard errors for the total earthworm numbers (all life cycle stages combined) are given for each month. * indicates the presence of cocoons.

Gemascolex walkeri Jamieson (Megascolecidae) was common at Tungkillo, not found at Parawa and occurred in only negligible numbers at Birdwood (Fig. 1, Table 1). *Aporrectodea rosea* (Savigny) (Lumbricidae) was most common at Birdwood and was also found at Tungkillo. *Octolasion cyaneum* (Savigny) (Lumbricidae) was found at Parawa but not at the other two sites. The abundances of *G. walkeri*, *A. rosea* and *O. cyaneum* varied between months (Kruskal-Wallis $H = 54.9$, $p < 0.001$ for *G. walkeri* at Tungkillo; $H = 42.3$, $p < 0.001$ for *A. rosea* at Birdwood; $H = 45.1$, $p < 0.001$ for *O. cyaneum* at Parawa), with highest numbers found from late winter to early spring (August to September or October) (Fig. 1). Other species were generally recorded in low numbers at the three sites (Table 1). *Gemascolex lateralis* (Spencer)

(Megascolecidae) was abundant at parawa in May and June 1990 (Table 1), but most of the individuals of this species collected then were found in only one sample in each month (53% of the total collection in May and 69% in June). There was no significant variation between months in the abundance of *G. lateralis* at Parawa ($H = 8.6$, $p > 0.05$).

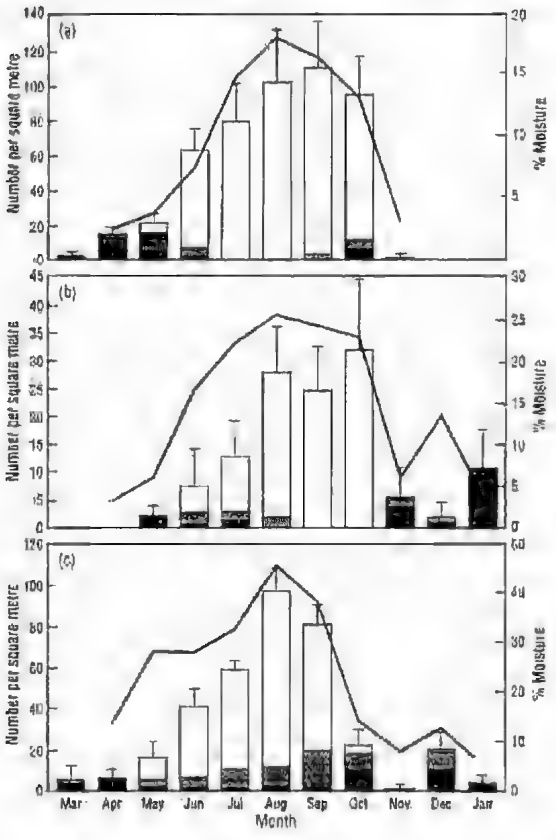

Fig. 2. Numbers (m^{-2}) of *Gemascolex walkeri* (Tungkillo) (a), *Aporrectodea rosea* (Birdwood) (b) and *Octolasion cyaneum* (Parawa) (c) collected 0-10 cm ( ), 10-20 cm ( ) and 20-30 cm ( ) below the soil surface during 1990-91. Standard errors for the total earthworm numbers (all depths combined) are given for each month. Mean gravimetric soil moistures for 0-10 cm deep are also indicated for each site (line).

Adults of *G. walkeri* and *A. rosea* were mostly collected in early spring (Fig. 1). Adults of *O. cyaneum* were present on most sampling occasions.

Earthworm cocoons were found at all three sites, during each month from July to October (up to 39 cocoons per soil sample).

Virtually all the cocoons (> 99%) were found in the top 10 cm of soil. The identity of these cocoons is unknown. Most of the cocoons probably belonged to *Aporrectodea trapezoides*, the most abundant species at these sites (Baker *et al.* 1992b). However, the breeding seasons of all species can be regarded as occurring within these months.

Depth Profile

G. walkeri, *A. rosea* and *O. cyaneum* occurred mainly in the root zone (0-10 cm depth) for four to five months during autumn to spring, when soils were wettest (Fig. 2) (Pearson $r_g = 0.98$, $r_{10} = 0.86$ and $r_{30} = 0.94$ for soil moistures and numbers of *G. walkeri* (Tungkillo), *A. rosea* (Birdwood) and *O. cyaneum* (Parawa) respectively at 0-10 cm depth; $p < 0.01$ in all cases). Earthworms became more common in the root zone compared with lower depths during May or June and less so in October or November.

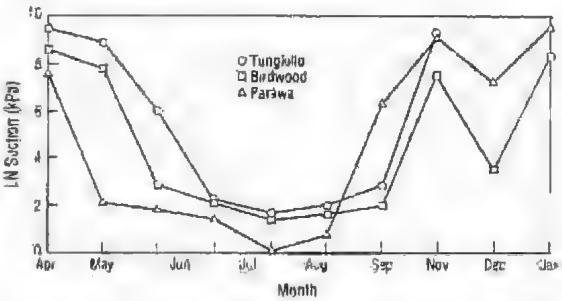

Fig. 3. Matric suctions of soil water (kPa) at 0-10 cm depth at Tungkillo (○), Birdwood (□) and Parawa (△).

The surface soil was moister in autumn (May) and drier in spring (October) at Parawa compared with the other two sites (Fig. 3). Proportionally more worms were present in the top 10 cm of soil at Parawa in May and less in October than at Tungkillo and Birdwood (Fig. 2, Table 1) (comparing the total earthworm numbers at 0-10 cm and 10-30 cm depth at each site for all species included in Table 1 and Fig. 2, $\chi^2 = 70.65$, $p < 0.001$ and $\chi^2 = 96.91$, $p < 0.001$ for May and October respectively).

Distribution Within Plots

The distributions of some species at each of the three sites were patchy. At Birdwood, *A. rosea* was most common in the south-eastern corner of the plot whilst *Gemascolex lateralis* and *G. stirlingi* occurred predominantly in the north-eastern corner (Fig. 4). The distribution of *A. rosea* approximated that of the black duplex soils at Birdwood (Fig. 4) ($\chi^2 = 16.25$, $p < 0.001$ where the samples with and without *A. rosea*

TABLE 1.
Numbers of earthworms collected in low numbers at three pasture sites in the Mt Lofty Ranges, South Australia. Numbers in parentheses are for earthworms in the top 10 cm of soil, * indicates adults were present and – that no samples were taken.

Species	Month											
	M	A	M	J	J	A	S	O	N	D	J	Total
Aporrectodea rosea												
Tungkillo	3	2	26 (7)	2	6 (6)	4* (4)	1* (1)	6* (6)	10* (3)	–	–	60
Microscolex dubius												
Tungkillo						4* (4)	14* (14)	8* (8)		–	–	26
Birdwood						2* (2)						2
Parawa							1* (1)					1
Gemascolex stirlingi												
Tungkillo					4* (2)	*1				–	–	5
Birdwood	1	1	3*	1	6 (5)	1	2 (1)	1 -	1	2	1	20
G. lateralis												
Tungkillo					1 (1)					–	–	1
Birdwood	5		4*	1 (1)	4 (4)	10 (10)	3 (3)	1 (1)	2	3		33
Parawa	3	6	53* (53)	78* (78)	17* (17)	14* (14)	9* (9)	3* (1)	21*	6*	19*	229
G. walkeri												
Birdwood							3* (3)			3		6
Native W												
Tungkillo		1*		1 (1)		1 (1)	1 (1)	2 (2)		–	–	6
Native J												
Birdwood									11*			11

within the areas with yellow and black duplex soils were compared), but the distributions of the two *Gemascolex* spp. could not be explained by variation in soil type.

At Tungkillo, *G. walkeri* was most abundant near the centre and eastern end of the plot (Fig. 5a) (χ^2 = 31.29, $p < 0.001$ where the frequencies of samples with 0, 1-5, 6-10 and > 10 earthworms inside and outside the area in Fig. 5a were compared). The soil within the area where *G. walkeri* was most common was moister in late summer than the soil outside it (Table 2). During the wettest months of the year, the same trend was also apparent. Mean soil moistures for the samples taken at 0-10 cm depth during the routine monitoring at Tungkillo from July to October 1990 were 17.2% (where *G. walkeri* was most common) and 13.1% (elsewhere) ($t = 2.23$, $p < 0.05$).

G. lateralis was mostly found in the south-eastern corner of the plot at Parawa (Fig. 5b) (χ^2 = 62.05, $p < 0.001$ where the frequencies of samples with 0, 1-5 and > 5 earthworms inside and outside the shaded area in Fig. 5b were compared). There was no obvious variation in habitat within the plot that might explain this patchiness in *G. lateralis*. However, several *Eucalyptus* trees bordered the plot adjacent to the area where *G. lateralis* was found. Perhaps these remnants of natural vegetation are responsible for local survival of this native earthworm.

Discussion

The life histories, patterns in seasonal abundance and depth profiles of *G. walkeri*, *A. rosea* and *O. cyaneum* in pastures in the Mt Lofty Ranges, South Australia are broadly similar to those reported previously for *A. trapezoides* and *A. caliginosa* (Baker *et al.* 1992b). Earthworm activity in the pasture root zone (0-10 cm depth) is mostly restricted to winter and early spring when soils are wettest. Adult earthworms are most commonly found in late winter-early spring, but for some species (e.g. *O. cyaneum* and *G. lateralis*), adults can be found during most months of the year.

The proportions of *A. rosea*, *O. cyaneum* and *Gemascolex* spp. populations that survive summer are not known, but many of these earthworms have been

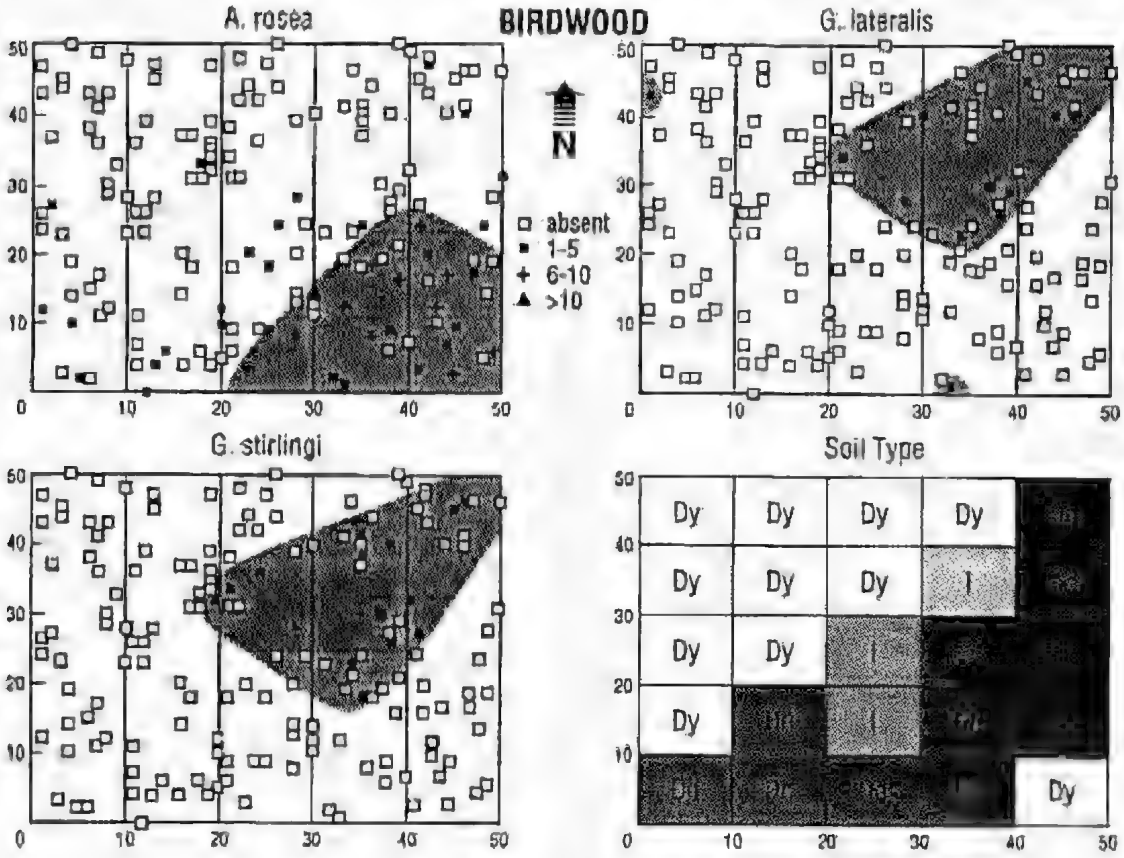

Fig. 4. Distributions of *Aporrectodea rosea*, *Gemascolex lateralis*, *G. stirlingi* and soil types at Birdwood. Earthworm numbers are given as 0 (□), 1-5 (■), 6-10 (+) and > 10 (▲) per sample. Shaded areas indicate where all or the majority of earthworms were found. Soil types were classified as yellow duplex (Dy), black duplex (Dd) and intergrade of Dy and Dd (I).

found in summer > 30 cm below the surface of the soil (G. Baker, unpublished data). The increase in population numbers that occurs in the surface layers of the soil in autumn and early winter must be explained by invasion of individuals from lower depths rather than by breeding, since no cocoons were found at that time.

Whilst pastures in the Mt Lofty Ranges are dominated by introduced lumbricids, especially *Aporrectodea* spp. (Baker *et al.* 1992a), some native megascolecids, such as *G. walkeri*, can be locally abundant and constitute a significant proportion of the total earthworm population. For example, *G. walkeri* constituted 40.1% of the total population collected at Tungkillo in 1990 (Baker *et al.* 1992b). [Most (54.8%) of the earthworms found at this site were *A. trapezoides*.] The contribution that native species make to soil structure and fertility has yet to be resolved. Experiments are currently being conducted to evaluate the role of *G. walkeri* at Tungkillo in burying surface-applied lime and offsetting soil acidity.

A. rosea is one of the most widespread and abundant earthworm species in South Australia and western Victoria (Baker *et al.* 1991, 1992a). Multiple regressions of the abundance of *A. rosea* against a variety of environmental variables have shown that soil particle size is statistically the most important regressor for sites in the Mt Lofty Ranges, as is the case for the other most common introduced species, *A. trapezoides* and *A. caliginosa* (Baker *et al.* 1992a). In general, the abundance of these earthworms increases with % clay content. Variations in soil particle size helped explain differences in the abundance of *A. trapezoides* and *A. caliginosa* at several farms including Tungkillo, Birdwood and Parawa (Baker *et al.* 1992b). They may also explain the differences in abundance reported here for *A. rosea* at Tungkillo and Birdwood. *A. rosea* was more abundant in the black duplex soil (19% clay) than in the yellow duplex soil (7% clay) at Birdwood and the uniform sand at Tungkillo (also 7% clay). The absence of *A. rosea* from Parawa (where clay content was 14%) is, however, not explained by clay content.

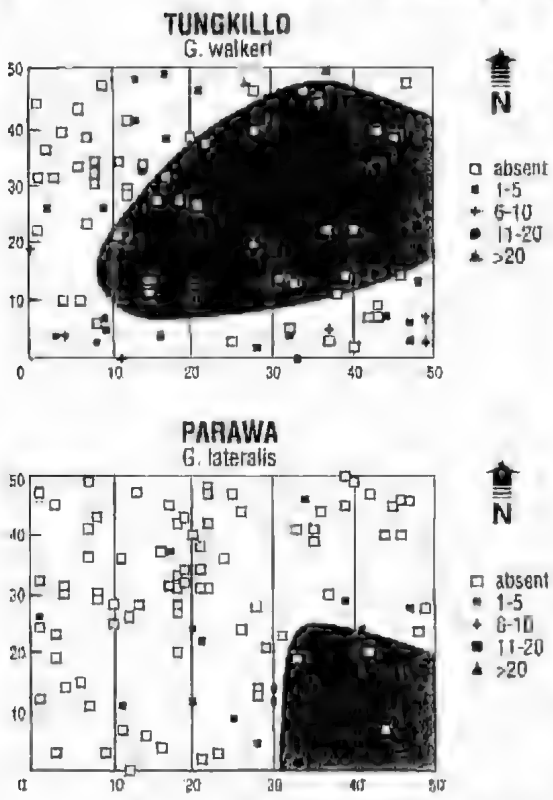

Fig. 5. Distributions of *Gemascolex walkeri* at Tungkillo and *G. lateralis* at Parawa. Earthworm numbers are given as 0 (□), 1-5 (■), 6-10 (+), 11-20 (●) and > 20 (▲) per sample. Shaded areas indicate where the majority of earthworms were found.

O. cyaneum was restricted to Parawa, the wettest site with an annual rainfall of 900 mm, compared with 575 and 750 mm at Tungkillo and Birdwood respectively. Previous surveys (Baker *et al.* 1991, 1992a) have found *O. cyaneum* at only a few sites in the highest rainfall regions of South Australia and western Victoria. There are a few records of *O. cyaneum* in Western Australia, all from the high rainfall region of the south-west (Abbott 1981). Sims & Gerard (1985) comment that *O. cyaneum* prefers moist habitats in Britain.

TABLE 2.
Gravimetric moistures (%) for soils collected at Tungkillo in March 1991.
Soils were collected at varying depths inside and outside the area in which *Gemascolex walkeri* was most abundant (see Fig. 5). Results of t tests for significant differences between data are included.

Depth (cm)	Soil Moisture Inside	Outside	t	Prob.
0-10	1.48	0.93	5.20	< 0.001
10-20	2.60	1.07	4.65	< 0.001
20-30	3.83	1.79	5.00	< 0.001
30-40	4.74	2.55	3.78	< 0.01
40-50	6.42	2.82	2.80	< 0.05

The distributions of the native species within the three sites were patchy. In some cases, possible reasons for the patchiness can be offered. For example, *G. walkeri* may be restricted by soil moisture at Tungkillo.

Baker *et al.* (1992b) reported minor levels of parasitism of *A. trapezoides* and another introduced earthworm, *Microscolex dubius*, at Tungkillo during spring by an undescribed dipteran. *G. walkeri* was more abundant than these other two species in the top 10 cm of soil at the same time, but was not parasitised.

Acknowledgments

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VOL. 117, PART 2

THE EARLY CAMBRIAN VOLCANICS FROM RED CREEK, EASTERN MT LOFTY RANGES, SOUTH AUSTRALIA

BY C. G. GATEHOUSE, J. B. JABO†, B. J. CLOUGH* & A. J. MCCULLOCH*†*

Summary

In the Red Creek area of the eastern Mt Lofty Ranges, Early Cambrian lavas, tuffs and volcaniclastic sediments are interbedded with the top 270 m of the Heatherdale Shale, the top member of the Normanville Group. Tuffs and volcaniclastic siltstones extend up into the basal 60 m of the conformably overlying Carrickalinga Head Formation, the basal unit of the Kanmantoo Group. Several lava flows of trachybasalts, one of which exhibits pillows, occur about 100 m below the top of the Heatherdale Shale. The volcanics at Red Creek appear to be at a slightly higher stratigraphic level than the Truro Volcanics, the type section of which is 24 km to the NNW of Red Creek. It is proposed that the lavas at Red Creek represent a flow of hawaiite composition from a central volcanic complex, closely analogous to that of the Truro Volcanics but not necessarily from the same centre or erupted at exactly the same time. Geochemical data indicate that both the volcanics at Red Creek and the Truro Volcanics belong to the same alkaline Early Cambrian "within plate" volcanic province, which may be linked genetically with other Cambrian mafic alkaline provinces such as the Yumali/Coonalpyn area. It is suggested that the closest tectonic analogy for these provinces is that of a rifted continental margin as proposed for the Tertiary intraplate volcanic province of eastern Australia.

KEY WORDS: Early Cambrian volcanics, hawaiite, Mt Lofty Ranges, Normanville Group, Kanmantoo Group

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THE EARLY CAMBRIAN VOLCANICS FROM RED CREEK, EASTERN MT LOFTY RANGES, SOUTH AUSTRALIA

by C. G. GATEHOUSE*, J. B. JAGO†, B. J. CLOUGH,* & A. J. MCCULLOCH*†

Summary

GATEHOUSE, C. G. JAGO, J. B., CLOUGH, B. J. & MCCULLOCH, A. J. (1993) The Early Cambrian volcanics from Red Creek, eastern Mt Lofty Ranges, South Australia. *Trans. R. Soc. S. Aust.* 117(2), 57-66 4 June, 1993.

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KEY WORDS: Early Cambrian volcanics, hawaiite, Mt Lofty Ranges, Normanville Group, Kanmantoo Group

Introduction

This paper is a progress report on work on the Early Cambrian volcanics generally known as the Truro Volcanics of the eastern Mt Lofty Ranges. The Truro Volcanics are important in that, although they are limited both in stratigraphic and geographic extent, they represent the most extensive outcrops of volcanics in the Cambrian sequences of the Stansbury Basin/Kanmantoo Trough area. As described below, volcanics in the Red Creek area extend from within the Heatherdale Shale, the top member of the Normanville Group, up into the Carrickalinga Head Formation, the basal member of the Kanmantoo Group. Hence a study of the Truro Volcanics is important in the determination of the stratotectonic setting of the Kanmantoo Group transition which has been interpreted in various ways as set out below.

Von der Borch (1980) considered the Kanmantoo Group sediments to be the initial phase of fully developed continental margin sedimentation which typified the eastern flank of cratonic Australia during most of the Palaeozoic. Turner & Foden (1990) suggested that this phase was marked by renewed mafic igneous activity in the form of the Truro Volcanics. The basal part of the Carrickalinga Head Formation at Carrickalinga Head lies north of Normanville where von der Borch (1980) proposed that the Houghton Anticlinal Zone acted as a separating feature between shallow-water sediments to the west and continental slope and rise environments to the east. Scheibner (1986, Fig. 4) implied that the Kanmantoo Group sediments were at least in part deposited on oceanic crust and that the "Kanmantoo Trough" was part of a marginal sea, extending eastwards to the Stavely volcanic belt of western Victoria. Parker (1986) suggested that the Kanmantoo Group sediments were probably deposited in an extensional tectonic regime on a marginal shelf reflecting tectonic activity to the west and a continental margin to the east. Powell (1990) regarded the "Kanmantoo Fold Belt" as representing the westernmost part of the "Tasman Fold Belt". He suggested that the Kanmantoo Group represents passive margin sedimentation.

The term Truro Volcanics was defined by Forbes *et al.* (1972) from a type section in Levi Creek, 11 km north of Truro (Fig. 1). They included two units within the Truro Volcanics (Fig. 2), with the lower unit comprising a 240 m thick sequence of interbedded volcaniclastic sediments, amygdaloidal volcanics and limestones. The upper unit as described by Forbes *et al.* comprises 60 m of marble, shaly marble, metasiltstone and a thin (2 m) horizon of porphyritic andesite. Forbes *et al.* (1972) noted that this sequence is overlain by the Heatherdale Shale which, near the base, contains clasts of volcanic rocks. However, the exact nature of the contact is unclear due to poor exposure. The Heatherdale Shale, the top unit of the Normanville Group, is overlain by the Carrickalinga Head Formation, the basal unit of the Kanmantoo Group. Forbes *et al.* (1972) suggested that the marble in the upper member of the Truro Volcanics is

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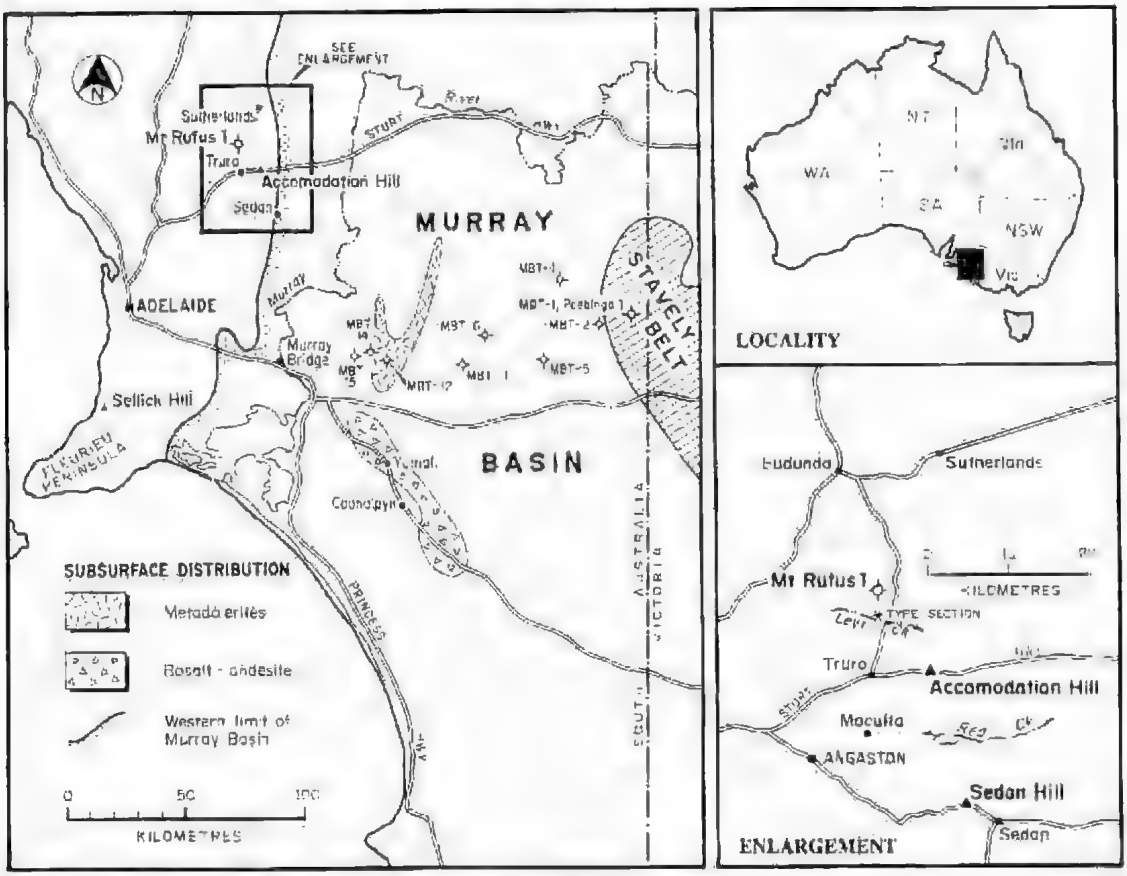

Fig. 1. Locality Map. The type section of the Truro Volcanics is 2 km south of Mt Rufus 1.

equivalent to the Fork Tree Limestone which at Sellick Hill conformably underlies the Heatherdale Shale (Daily 1963).

Rocks assigned to the Truro Volcanics by previous workers occur in outcrop only in the Karinya Syncline, north-east of Adelaide as shown by Cobb & Farrand (1984). A recent report which may extend the known distribution of the Truro Volcanics is that of Polomka (1988)[1] who reported float material of possible Truro Volcanics about 2 km NNE of Moculta, near the base of what he mapped as Carrickalinga Head Formation. However, the exact stratigraphic position of these rocks is doubtful because of the poor outcrop in the area. Polomka described the rock as comprising fine to medium grained phenocryst pseudomorphs of epidote (2%), within a very fine actinolite (45%) and epidote (30%) groundmass.

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[8]Rankin, L. R., Clough, B. J., Farrand, M. G., Barnett, S. R., Lablack, K. Gatehouse, C. G. & Hough, L. P. (1991b) Murray Basin basement transect project: 1990 well completion reports. *S. Aust. Dept Mines & Energy Rept Bk* **91/25**.

TRURO VOLCANICS TYPE SECTION

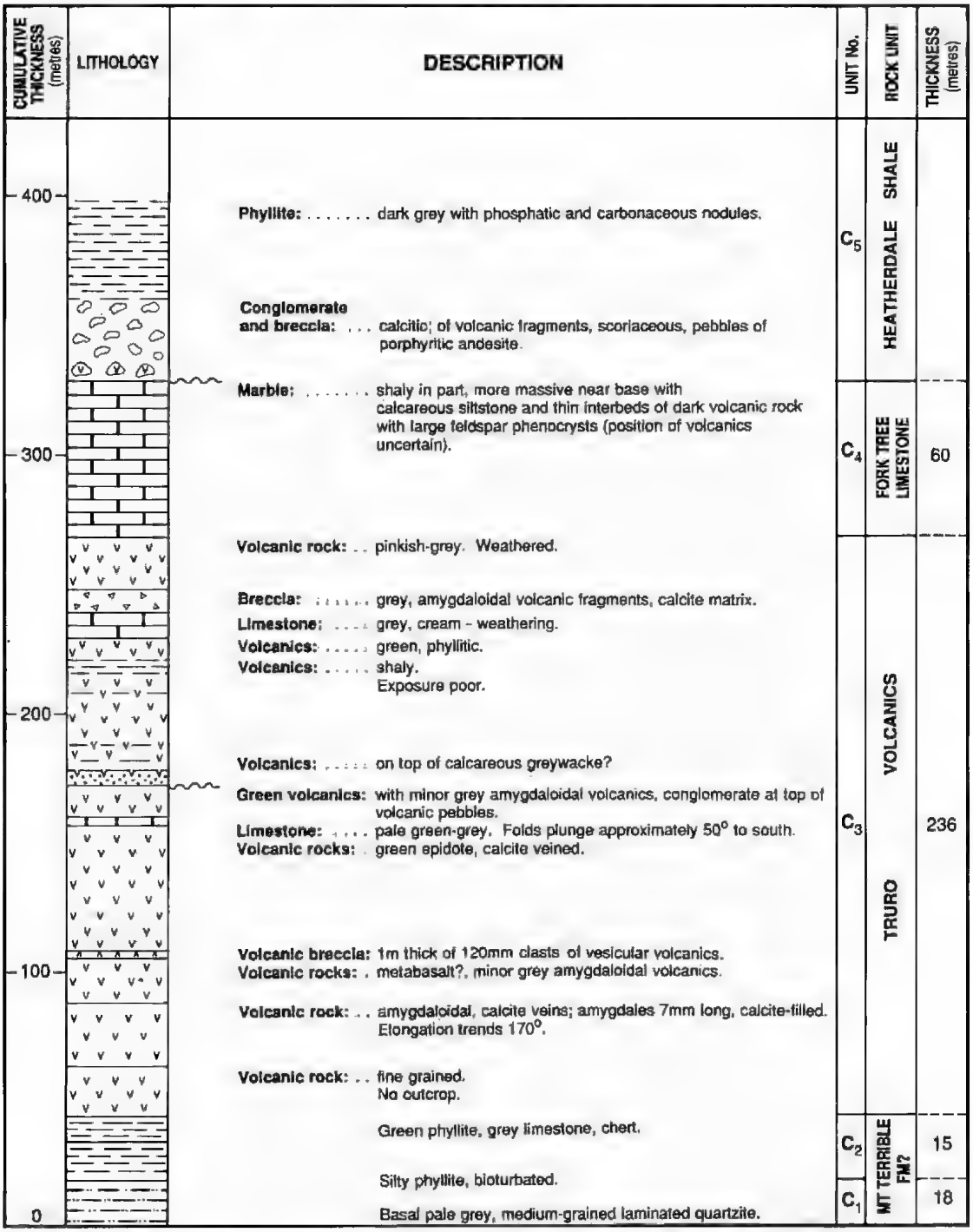

Fig. 2. Stratigraphic section at type section of Truro Volcanics, 11 km north of Truro (after Forbes *et al.* 1972).

At the extreme eastern edge of the Mt Lofty Ranges, Early Cambrian volcanics have been recorded at Sedan Hill (Cooper & Gatehouse 1988[2]; Gatehouse *et al.* 1990), at Red Creek (Gatehouse *et al.* 1991a[3]; McCulloch 1990[4]; Van der Stelt 1990[5]), Accomodation Hill (Forbes *et al.* 1972) and near Sutherlands (Forbes *et al.* 1972). The best exposure of Early Cambrian volcanics from the eastern Mt Lofty Ranges are those mapped in Red Creek by Coats & Thomson (1959) as feldspar porphyrite. The remainder of this paper deals largely with the Red Creek area, north-west of Sedan (Fig. 1).

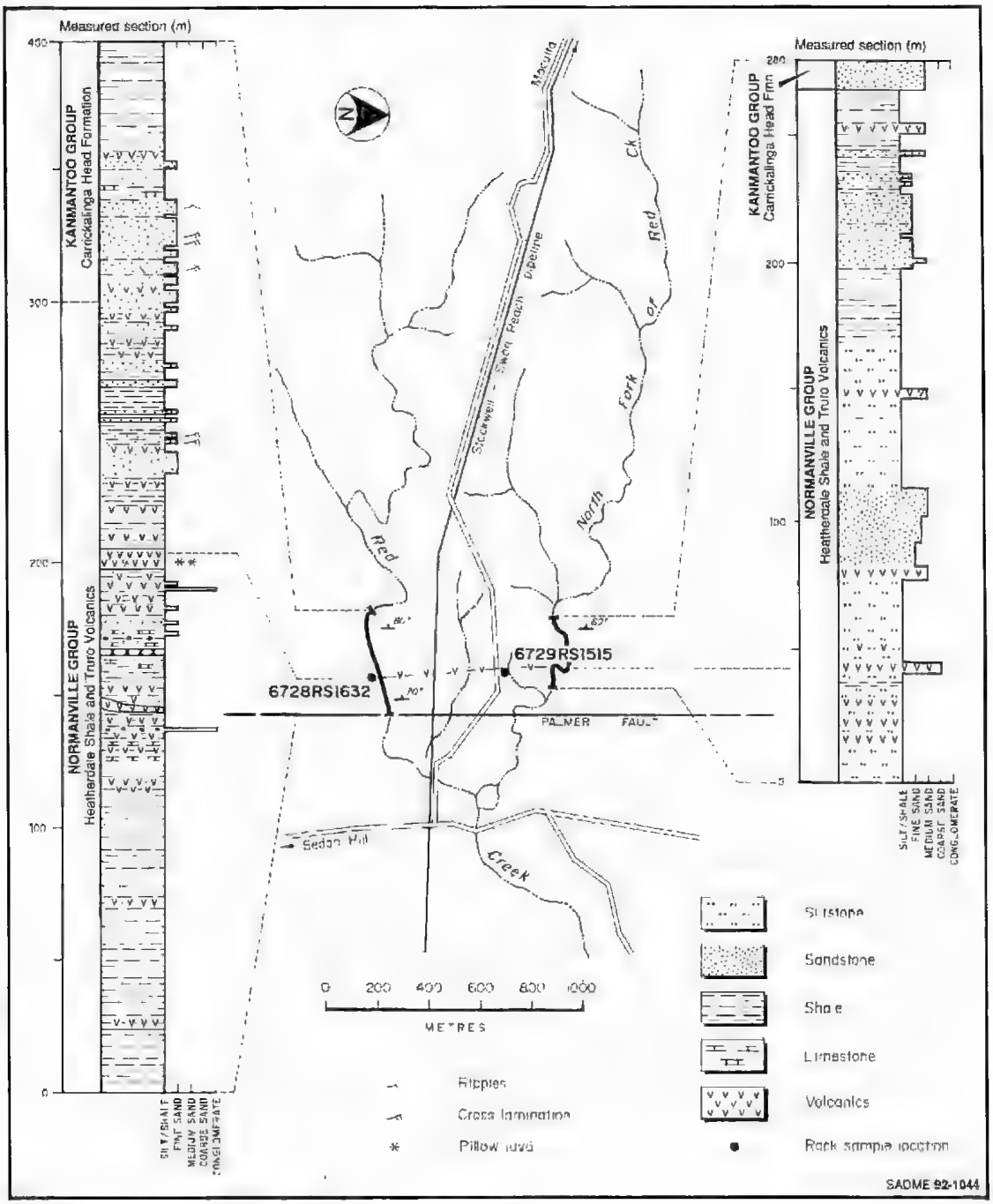

Fig. 3. Stratigraphic section at Red Creek.

Stratigraphic setting

Detailed measured sections at Sedan Hill (Cooper & Gatehouse 1988) and at Red Creek (Gatehouse *et al.* 1991a[3]) show that volcanic rocks, generally referred to as the Truro Volcanics are interbedded within the Heatherdale Shale and continue into the basal parts of the gradationally overlying Carrickalinga Head Formation. The Red Creek section has been logged in some detail (Gatehouse *et al.* 1991b[6]); only a summary of the section is given here (Fig. 3).

About 300 m of Heatherdale Shale is exposed at Red Creek; the base is not exposed due to the presence of the Palmer Fault. As exposed at Red Creek the Heatherdale Shale is a pale grey laminated phyllite which becomes darker and less micaceous up-section. There are minor calcareous siltstone horizons. Within these units are thin tuffaceous and/or volcanogenic siltstone horizons which become increasingly abundant up-section.

About 200 m above the base of the measured section are several basaltic lava flows, one of which exhibits pillows (Fig. 4). The pillowed flow has an uneven base and cuts down into an underlying 0.2 m thick tuff horizon; it appears to thin to the south. It contains several pillow structures with chilled margins and triple junctions (Fig. 4). An intrusive igneous body seen between 145 and 150 m on the measured section may represent a feeder pipe to the lavas higher in the section. Above the pillow lavas the tuffaceous/volcanogenic siltstone horizons continue with reduced frequency into the basal 60 m of the gradationally overlying Carrickalinga Head Formation. Detailed descriptions of the complete stratigraphic section will be given in a later paper.

In the north branch of Red Creek (Fig. 3), close to the base of the Carrickalinga Head Formation, there are several beds, and/or blocks, of crystal tuff comprising almost pure feldspar crystals clearly winnowed from enclosing ash. Such beds may have formed by current activity at the site of deposition or by differential air-fall separation.

Fig. 4. Pillow lavas at Red Creek. Note the triple junction at centre left.

Regional stratigraphic interpretation

As noted above, in Red Creek, lavas and volcanogenic sediments extend thorugh the exposed Heatherdale Shale up into the base of the Carrickalinga Head Formation. However, near the type section (Fig. 2) of the Truro Volcanics 24 km NNW of Red Creek, the highest known volcanics are at least 200 m below the top of the Heatherdale Shale (see map in Forbes *et al.* 1972 and Fig. 2 herein). Indeed Forbes *et al.* (1972) suggest that the bulk of the volcanics in the type area occurs below an equivalent of the Fork Tree Limestone, which on Fleurieu Peninsula lies conformably below the Heatherdale Shale. However, since this correlation with the Fork Tree Limestone is made on lithological grounds only, and further, that there are calcareous horizons within the Heatherdale Shale both on Fleurieu Peninsula and at Red Creek, then there may be some doubt about the correlation. It could be argued that the marble of the type area of the Truro Volcanics, described as Unit C4 by Forbes *et al.* (1972), is equivalent to the calcareous horizons found in the Heatherdale Shale at Red Creek rather than being equivalent to the Fork Tree Limestone. However, if the correlation of the Unit C4 marble in the type section to the Fork Tree Limestone is correct then it suggests that the volcanics at Red Creek are in a higher stratigraphic position than those of the type section and should not be referred to the Truro Volcanics. In his discussion on the Stansbury Basin, Gravestock (in press) has included all these volcanics as Truro Volcanics. A further complication is the almost complete lack of exposure of the basal 150 m of the Heatherdale Shale near the type section of the Truro Volcanics. The recent drilling of Mt Rufus No. 1 stratigraphic hole 2 km north of the type section suggested that there may be several unrecognised faults in the area (Gatehouse *et al.* 1991b[6]). Until the position is clarified the volcanics described herein are simply referred to as the volcanics from Red Creek.

Elsewhere in the Stansbury Basin, green tuff beds in the Parara Limestone may be correlated with the Truro Volcanics of the Karinya Syncline (Gravestock in press). A tuff bed from within the Heatherdale Shale at Sellick Hill has been dated at 526±4 Ma (Cooper *et al.* 1992); this tuff may also be equated with the Truro Volcanics or the volcanics at Red Creek or with neither.

Petrography of volcanics at Red Creek

In hand specimens the volcanics in Red Creek have a grey fine grained ground mass with distinctive large

(approximately 0.5 mm diameter) phenocrysts of feldspar (up to approximately 25%) and minor iron staining. The rocks show variable intensities of tectonic foliation.

In thin section it appears that the phenocrysts are predominantly of zoned plagioclase although approximately 10% of the phenocrysts are of an alkali feldspar. The groundmass is predominantly of acicular feldspar laths producing a trachytic texture. The tectonic fabric of these rocks varies from slight to intense foliation, the feldspar phenocrysts having rotated parallel to the foliation. Alteration is pervasive with sericitisation of the feldspar and chlorite/iron-oxide replacement of mafic minerals. Sporadic veinlets of quartz and calcite cross-cut this rock. Petrologically the lavas classify as trachytic basalt.

Geochemistry of volcanics at Red Creek

Two samples (6728 RS 1632 and 6729 RS 1515) of massive pillow lava were taken from separate localities near Red Creek and geochemically analysed for a comprehensive suite of elements (Tables 1 and 2). Several analytical methods were used, including:

ICP (acid digestion) — major elements
XRF — As, Ba, Bi, Sb, Sn, V, Zr
Atomic Absorption Spectrography — Ag, Cr, Cu, Ni, Pb, Zn
Fire Assay — Au, Pt, Pd
ICP Mass Spectrography — Ce, Dy, Nd, Er, La, Eu, Lu, Yb, Y, Sm, Gd, U, Th, Sr, W, Ta, Mo, Nb, Ga, Co, Cs, Rb.

The two geochemical analyses (Tables 1 and 2) of the pillow lava reflect their described lithology, as basaltic lavas that have undergone greenschist facies metamorphism. Elevated loss on ignition (LOI) values (average 11.5%) attest to alteration effects resulting in hydration. Clearly the present chemical composition of the lavas at Red Creek is not primary, as the volatile content is significantly higher than in analogous fresh rocks. This is to be expected from the presence of

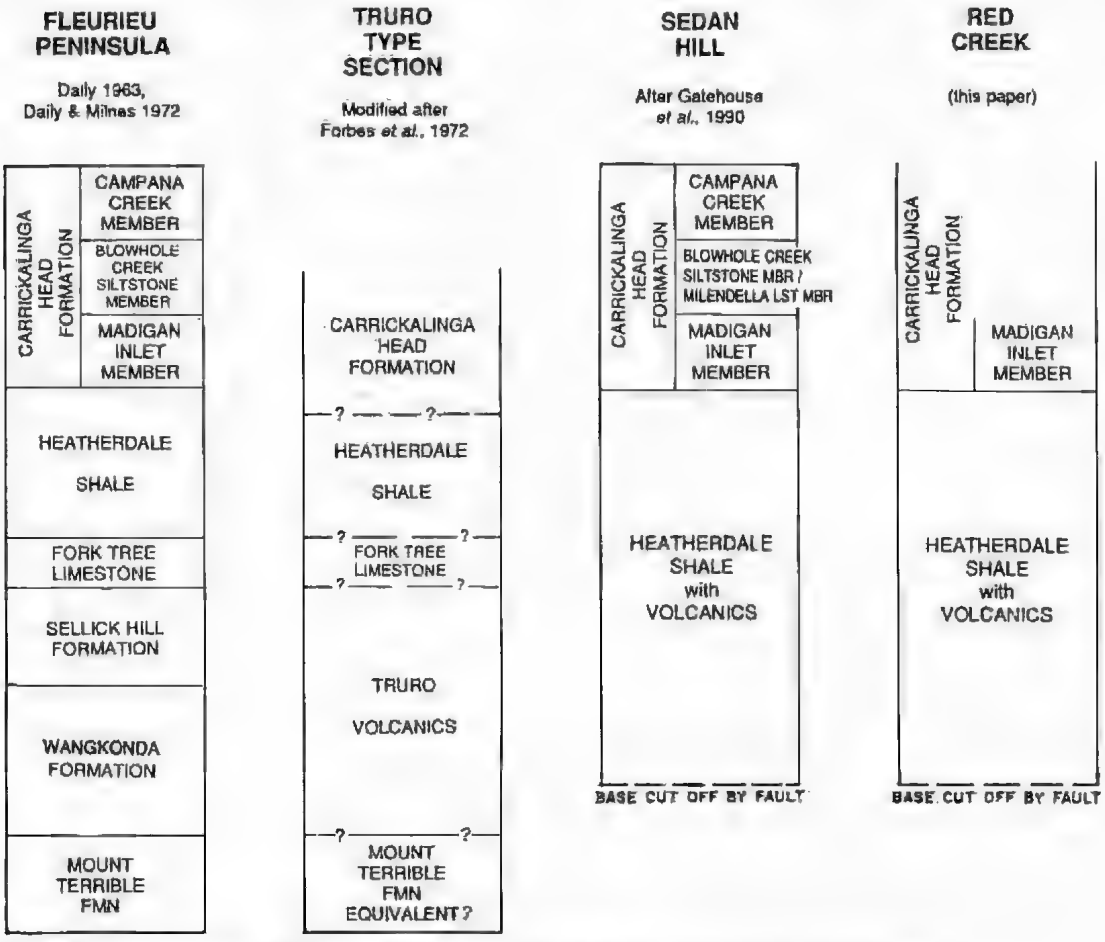

Fig. 5. Correlation diagram of the Cambrian sequences of the Red Creek-Truro-Sellick Hill areas

TABLE 1. Geochemical analyses and CIPW norms. N.B. CIPW weight % norms are calculated from analyses recalculated to 100% free of H_2O and CO_2; cc is not recalculated, Fe data is recalculated using a Fe_2: Total Fe cation ration of 0.20.

Major Elements in Percent			CIPW Weight % Norms		
	6728 RS 1632	1515		6728 RS 1632	1515
SiO_2	42.30	42.30	ab	18.85	19.92
TiO_2	2.42	2.24	or	19.71	13.69
Al_2O_3	15.80	14.40	an	18.47	15.31
Fe_2O_3	8.75	8.05	ne	9.85	13.22
FeO			di	18.11	23.15
MnO	0.28	0.26	ol	4.67	3.21
MgO	2.64	3.32	mt	2.94	2.72
CaO	8.05	8.85	il	5.32	4.95
Na_2O	3.78	4.50	ap	2.09	1.73
K_2O	2.88	1.99			
P_2O_5	0.78	0.66	Total	100.01	100.01
H_2O+					
H_2O					
CO_2					
LOI	10.80	12.30			
Total	98.48	98.87	DI	48.41	46.82

=not analysed, DI=Differentiation Index

hydrous secondary minerals in these lavas. Similar alteration of mafic lavas in the Victorian greenstone belts (Crawford & Keays 1978) is considered to have caused hydration, along with slight addition of CO_2 and Na_2O accompanied by leaching of SiO_2, CaO, Al_2O_3 and K_2O. However, the degree of chemical change was considered to be minimal, and magmatic trends were clearly visible. To minimise the effect of hydration dilution and related chemical mobility, plots using elements considered immobile during alteration are used and analyses are recalculated to 100% volatile-free prior to plotting.

The lava at Red Creek plot on the border between phono-tephrite and tephrite-basanite close to the basaltic-trachyandesite field in the SiO_2 versus Na_2O+K_2O classification plot of Le Bas *et al.* (1986; Fig. 6). In the Nb/Y versus Zr/TiO_2 classification plot (Winchester & Floyd 1977; Fig. 7) using elements considered immobile during alteration, the lavas classify as alkali basalt.

To further define the alkaline basalt a classification scheme devised for the Tertiary alkaline volcanics of eastern Australia (Johnson 1989) based on CIPW norms was utilised (Fig. 8). Using this classification scheme the division between sub-alkaline and alkaline mafic lavas is that alkaline lavas have <10% normative hypersthene; on this basis the basalts in Red Creek classify as alkaline and plot within the field of hawaiites. The presence of considerable levels (9.85 and 13.22%) of normative nepheline suggests these rocks are silica undersaturated. However, plots using immobile elements (Fig. 7) suggest these lavas have not attained silica undersaturation but show that the lavas at Red Creek and the Truro Volcanics at Mt Rufus 1 (Gatehouse *et al.* 1991b[6]) belong to a group of analyses that straddle the boundary between alkali basalt and silica undersaturated nepheline/basanite fields.

The analyses agree with field evidence suggesting that the lava at Red Creek represents a single thin submarine lava sequence from a common source, in that they plot close together on all classification plots.

The lavas plot outside the tectonic discrimination fields of Pearce & Cann (1973; Fig. 9), although closest to the intraplate field; and in marked contrast to the MORB-related metadolerites that occur in the Murray Basin basement (Rankin *et al.* 1991a, b[7,8]) and as sills and dykes in the Mt Lofty Ranges (Liu & Fleming 1990; Rankin *et al.* 1991a[7]). On a MORB normalised spidergram (Fig. 10) the Red Creek lava shows a distinctive trend of elemental enrichment relative to MORB values of the incompatible elements from Sr through to Ni, which is typical of the more silica

TABLE 2. Trace elements in ppm.

	6728 RS 1632	6729 RS 1515	Detection limit (ppm)
Ag	<1.00	<1.00	1
As	64.00	72.00	2
Au	2.00B	7.00B	)B
Ba	880	610	10
Bi	4.00	<4.00	4
Ce	82.00	78.00	0.1
Co	29.00	44.00	1
Cr	110	105	4
Cs	1.80	1.20	0.2
Cu	6.00	5.00	2
Dy	8.00	7.20	0.1
Er	3.90	3.30	0.1
Eu	2.80	2.50	0.1
Ga	26.00	20.00	1
Gd	9.00	8.60	0.1
La	38.00	36.00	0.1
Lu	0.60	0.50	0.1
Mo	4.00	3.55	0.5
Nb	76.00	66.00	0.5
Nd	44.00	42.00	0.1
Ni	52.00	54.00	4
Pb	12.00	12.00	4
Pd	1.00B	<1.00B	1B
Pt	<5.00B	<5.00B	5B
Rb	82.00	60.00	0.2
Sb	<4.00	4.00	4
Sm	9.60	8.80	0.1
Sn	<4.00	10.00	4
Sr	240	255	0.1
Ta	3.00	2.20	0.2
Th	4.80	3.60	0.1
U	2.60	2.20	0.1
V	<5.00	<5.00	5
W	3.00	3.00	1
Y	34.00	29.5	0.1
Yb	3.70	3.00	0.1
Zn	22.00	26.00	2
Zr	380	320	4

B=ppb

undersaturated alkaline mafic lavas of such provinces as the Tertiary eastern Australian volcanic province (Johnson 1989); note the marked contrast of the alkaline intraplate lavas with MORB related metadolerite from MB-12 in the Murray Basin basement (Rankin *et al.* 1991a[7] and b[8]).

Other alkaline volcanic areas similar to Red Creek include the Yumali/Coonalpyn area, the Peebinga-1 (MBT-1) drillhole into the northwestern termination of the magnetically defined Mt Stavely Belt (Rankin *et al.* 1991a[7], b[8]), and the Truro Volcanics as defined in Mt Rufus 1 drillhole (Gatehouse *et al.* 1991b[6]; Fig. 10). Of the other volcanics the nearest are the Truro Volcanics that crop out on the west limb of the Karinya Syncline 22 km NW of Red Creek; the lavas at Red Creek represent a more evolved lava type than the Truro Volcanics in their type section, resulting in a line more distant from MORB in Fig. 10. This chemical difference is seen in the petrology where the lavas at Red Creek are distinctively porphyritic with phenocrysts of alkali feldspar.

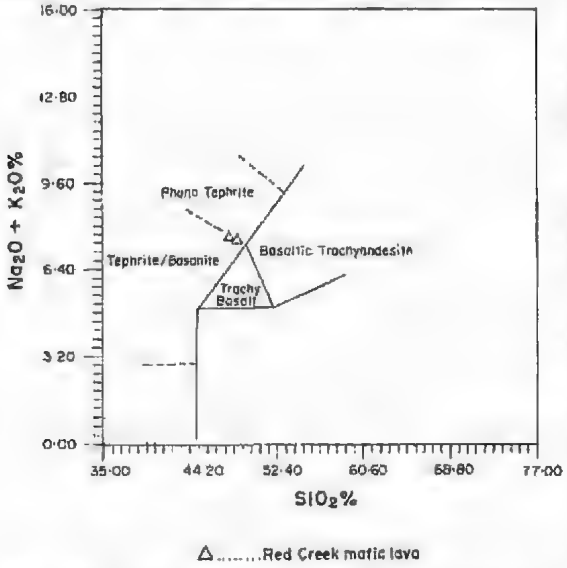

Fig. 6. Red Creek lavas on part of classification plot of Le Blas *et al.* (1986). Values calculated to 100% volatiles free.

The Red Creek analyses are compared with a classic continental intraplate volcanic suite in Fig. 11, where they are normalised to Karoo type basalts, the lavas at Red Creek and the other Cambrian alkaline volcanics noted above exhibit enrichments relative to Karoo basalt of the elements Sr to Ti, with Red Creek being one of the most chemically evolved suites. This supports the field relations which suggest that these lavas are not directly analogous to the thick piles of dominantly tholeiitic basalt fissure lavas of the Karoo Province, but rather are more closely analogous to the more localised central complexes seen in intraplate alkaline volcanic complexes (Johnson 1989).

In summary, it is proposed that the lava at Red Creek represents a single flow of hawaiite composition from a central volcanic complex, closely analogous to that of the Truro Volcanics but not necessarily from the

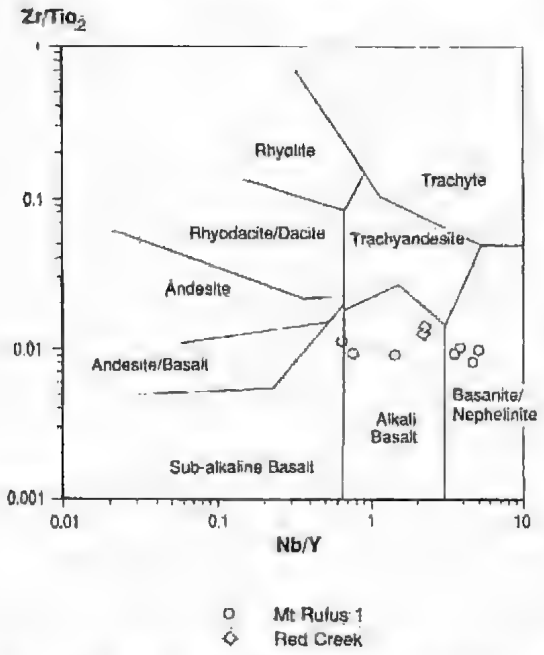

Fig. 7. Red Creek and Mt Rufus 1 lavas on part of classification plot of Winchester & Floyd (1977).

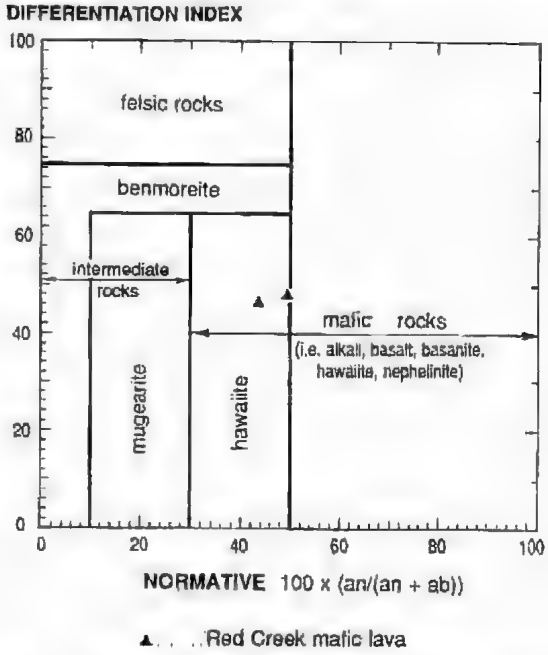

Fig. 8. Red Creek lavas on CIPW normative classification plot for sub-alkaline intraplate lavas (Johnson 1989).

same centre or erupted at exactly the same time. However, both the lava at Red Creek and the Truro Volcanics undoubtedly belong to the same Early Cambrian alkaline 'within plate' volcanic province, which may be genetically linked to other Cambrian-mafic alkaline provinces such as the Yumali/Coonalpyn and Peebinga-1 areas (Rankin *et al.* 1991a[7] and b[8]). The closest tectonic analogue for these provinces is that of a rifted continental margin as proposed for the Tertiary intraplate volcanic province of eastern Australia (Johnson 1989); metadolerites which post-date the volcanics indicate a change with time from intraplate to MORB type composition (Liu & Fleming 1990) indicating an ensuing period of crustal thinning and major dyke emplacement, associated rifting and crustal extension.

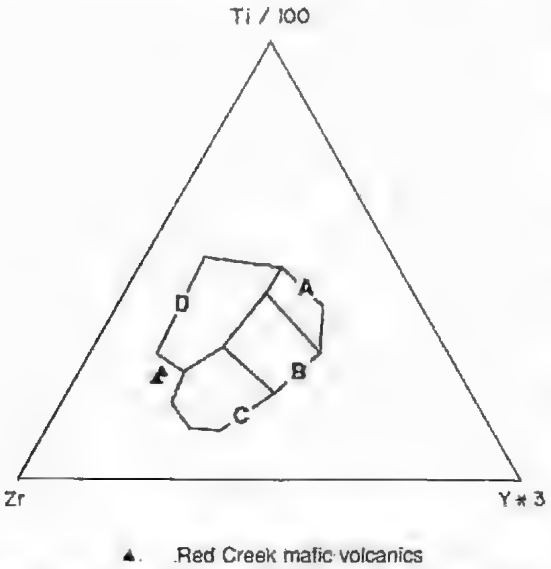

Fig. 9. Red Creek volcanics on tectonic discrimination plot of Pearce & Cann (1973). "Within plate" basalts plot in field D, Morb (ocean floor basalts) in field B, low Ktholeiites in field A and B, calc-alkaline basalts in fields C and B.

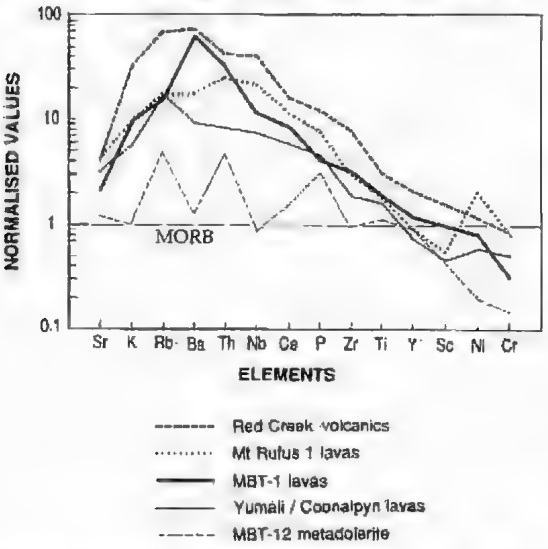

Fig. 10. MORB normalised spidergram for averages of possible Cambrian mafic suite from the Murray Basin basement and the Cambrian lavas of the Mt Lofty Ranges.

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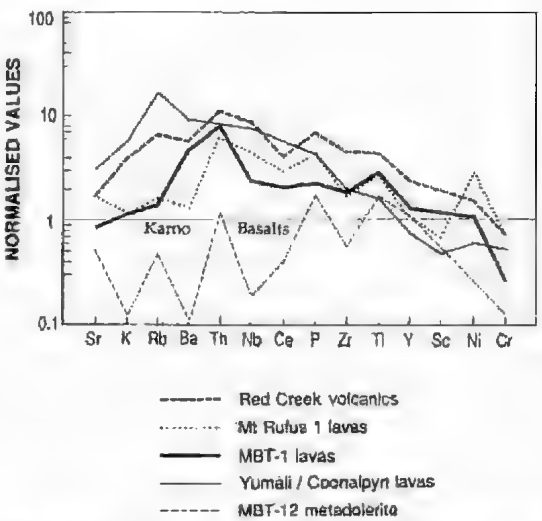

Fig. 11. Karoo Basalt normalised spidergram for averages of possible Cambrian mafic suites from the Murray Basin basement and the Cambrian lavas of the Mt Lofty Ranges.

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BIOLOGY OF ETIELLA BEHRII ZELLER (LEPIDOPTERA: PYRALIDAE): A PEST OF SEED LUCERNE IN SOUTH AUSTRALIA

*BY A. D. AUSTIN, T. C. R. WHITE, D. A. MAELZER & D. G. TAYLOR**

Summary

The general biology of the pyralid moth, *Etiella behrii* Zeller, a serious but sporadic pest of lucerne seed crops in South Australia, is documented. Larvae are recorded as feeding on six native and 18 introduced legume species. Head capsule widths of field-collected larvae show that *E. behrii,* like other pyralids, has five instars. Light-trap catches indicate the presence of at least four overlapping generations per year in the Adelaide area, with the majority of moths occurring during three generations from August to February. In lucerne crops in the Keith area, 150 km south-east of Adelaide, young and mature green pods suitable for oviposition are available from October to February. Two peaks in moth catches were recorded in late December and late January, respectively. Until mid-January, the number of eggs was strongly correlated with the numbers of moths caught, but thereafter the numbers of eggs and larvae decreased, with the second peak of moths giving rise to very few larvae. These observations are in agreement with the opinion of farmers that early lucerne crops are more heavily infested with *E. behrii* than late crops. Surveys of vegetation in the Keith area show that native host plants are very scarce, and that volunteer lucerne plants along road-sides and irrigation banks are the likely source of early infestations in Lucerne crops. Mortality agents recorded include ten species of parasitoids, two pathogens and a number of general heteropteran and spider predators. These and other possibilities are discussed as factors leading to the observed decrease in larval numbers in mid to late January, a time when lucerne crops still contain a large proportion of green pods suitable for larval development.

KEY WORDS: *Etiella behrii,* Pyralidae, ecology, life history, lucerne, alfalfa, host plants, parasitoids, predators, pathogens.

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BIOLOGY OF *ETIELLA BEHRII* ZELLER (LEPIDOPTERA: PYRALIDAE): A PEST OF SEED LUCERNE IN SOUTH AUSTRALIA

by A. D. Austin, T. C. R. White, D. A. Maelzer & D. G. Taylor*

Summary

Austin, A. D., White, T. C. R., Maelzer, D. A. & Taylor, D. G. (1993) Biology of *Etiella behrii* Zeller (Lepidoptera: Pyralidae): a pest of seed lucerne in South Australia. *Trans. R. Soc. S. Aust.* 117(2), 67-76, 4 June, 1993.

The general biology of the pyralid moth, *Etiella behrii* Zeller, a serious but sporadic pest of lucerne seed crops in South Australia, is documented. Larvae are recorded as feeding on six native and 18 introduced legume species. Head capsule widths of field-collected larvae show that *E. behrii*, like other pyralids, has five instars. Light-trap catches indicate the presence of at least four overlapping generations per year in the Adelaide area, with the majority of moths occurring during three generations from August to February. In lucerne crops in the Keith area, 150 km south-east of Adelaide, young and mature green pods suitable for oviposition are available from October to February. Two peaks in moth catches were recorded in late December and late January, respectively. Until mid-January, the number of eggs was strongly correlated with the numbers of moths caught, but thereafter the numbers of eggs and larvae decreased, with the second peak of moths giving rise to very few larvae. These observations are in agreement with the opinion of farmers that early lucerne crops are more heavily infested with *E. behrii* than late crops. Surveys of vegetation in the Keith area show that native host plants are very scarce, and that volunteer lucerne plants along road-sides and irrigation banks are the likely source of early infestations in lucerne crops. Mortality agents recorded include ten species of parasitoids, two pathogens and a number of general heteropteran and spider predators. These and other possibilities are discussed as factors leading to the observed decrease in larval numbers in mid to late January, a time when lucerne crops still contain a large proportion of green pods suitable for larval development.

Key Words *Etiella behrii*, Pyralidae, ecology, life history, lucerne, alfalfa, host plants, parasitoids, predators, pathogens.

Introduction

One of the most serious pests which can limit the production of lucerne seed in South Australia is *Etiella behrii* Zeller (lucerne seed web moth) (Maelzer *et al.* 1982a, 1982b; Durham 1984; Austin *et al.* 1986). It is one of seven species of *Etiella*, the larvae of which feed on the seeds of legumes (Whalley 1973). The most widespread and economically important species is the cosmopolitan *E. zinckenella* (Treitschke), a serious pest of legumes in many parts of the world, which in Australia is known only from Queensland (Abdul-Nasr & Awadalla 1957; Stone 1965; Singh & Dhooria 1971; Whalley 1973; Common 1990). The remaining six species are restricted to Australia, parts of south-east Asia and some Pacific islands. Only three species, *E. chrysoporella* Meyrick, *E. hobsoni* (Butler) and *E. behrii*, are recorded from South Australia; the former two only rarely as adults, and only from the northern and western parts of the State. The multivoltine *E. behrii* is a widespread and common pest throughout Australia, and of economic significance because of its heavy but sporadic outbreaks in dryland and irrigated crops of seed lucerne.

Little is known of the general biology or ecology of *E. behrii*, possibly because of its sporadic occurrence. In most years it does little damage to lucerne seed crops in S.A., but occasionally it causes widespread damage. At such times the species is also reported to damage lupins, field peas and some clovers, e.g. in 1954 and 1971 (Austin *et al.* 1986; DAM and DGT, unpubl.). *E. behrii* is thought to live on native plants along road-sides and in patches of scrubland during spring and early summer before infesting lucerne seed crops in mid summer, but this has not been confirmed. The present study was therefore undertaken to elucidate this part of its phenology and to document its general biology. Data have been included from a pest management program on lucerne seed crops (see Maelzer *et al.* 1982a, 1982b; Durham 1984), information collected in 1959-60 (by DGT), and life history studies undertaken during 1980-82.

Materials and Methods

Location of study

The project was centred on a property ('Brecon') 10 km south of Keith, S.A., in the middle of a major area of lucerne seed production. The area has a Mediterranean-type climate with mostly cold, wet winters and hot, dry summers (Anon. 1987). The

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average rainfall for the area is 471 mm per annum. The early (spring) dryland lucerne crops are watered naturally by rainfall, but the majority of the seed crops are managed to flower in mid-summer and are irrigated, mostly by flood irrigation rather than by sprinklers. Work in the Adelaide area, which has a similar climate to Keith, was carried out in 1959-60 and was centred at the Waite Institute campus of the University of Adelaide.

Trap catches of adult moths

Adults were caught at a light trap each night in two separate studies in widely different years: over the period 1.iii.1959 to 18.ii.1960 on the Waite Institute campus (by DGT) and from 1.xii.1981 to 20.ii.1982 at 'Brecon' (by DAM). The second period of trapping was part of a general program of sampling insects in lucerne seed crops (Maelzer *et al.* 1982a, 1982b). The light trap in 1959-60 was a mercury-vapour type, while that used in 1981-82 was a 15 watt blacklight type (cf. Hardstack *et al.* 1979), located in the middle of a lucerne area containing both dryland (early) and irrigated (late) crops.

Sampling eggs and larvae from lucerne crops

Five sampling sites were selected at 'Brecon' around a field of lucerne which was to be irrigated later that summer. All were dryland areas (i.e. not irrigated) and were of the commonly grown Australian cultivar, Hunter River. Each had been closed off to grazing animals some weeks earlier and contained lucerne plants with flowers and pods. Samples were collected from these sites about once per week from the beginning of December 1981 until mid January 1982 and taken back to the laboratory. Ten small samples (each of about 50 pods) were also taken from one or two more distant, dryland sites (up to 30 km away), including fields of lupins with volunteer lucerne plants.

Each sample was taken by walking through an area of 4-5 ha and picking stems of lucerne with flowers and pods from a number of widely spread points until 15-20 stems had been gathered. The stems were temporarily stored in a plastic bag on ice. In the laboratory each stem was searched, from the oldest raceme upwards, and each pod on each raceme was examined for eggs and larvae on the outside, and larvae inside. The procedure was continued until approximately 200 pods had been inspected. This meant searching from 1-12 stems ($\bar{x} = 5.0$; S.D. = 1.9) bearing from 1-11 racemes each ($\bar{x} = 5.3$; S.D. = 2.3). The racemes on any one stem were at any stage from unopened flowers to fully matured brown (dry) pods. All stages of flowers and pods were usually present on a single stem and, wherever possible, stems were selected that had some well-developed pods. For each raceme a record was made of the number of *E. behrii* eggs and larvae (classed as instars: 1 + 2, 3 + 4, or 5) and the stage of development of the pods (classed as flowers, pods just forming, juvenile pods, young pods, mature green pods and mature brown pods — see Fig. 1). In earlier samples, no stages of *E. behrii* had been found on flowers, on pods that were just

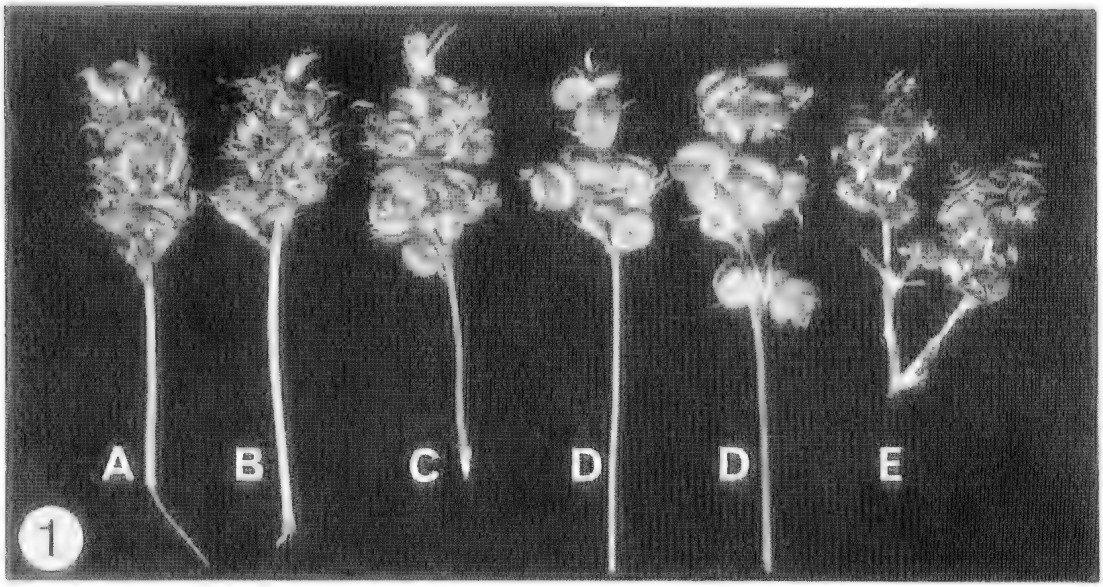

Fig. 1. Stages of pod development on lucerne plants: A, pods just forming; B, juvenile pods; C, young pods; D, mature green pods; E, mature brown (dry) pods.

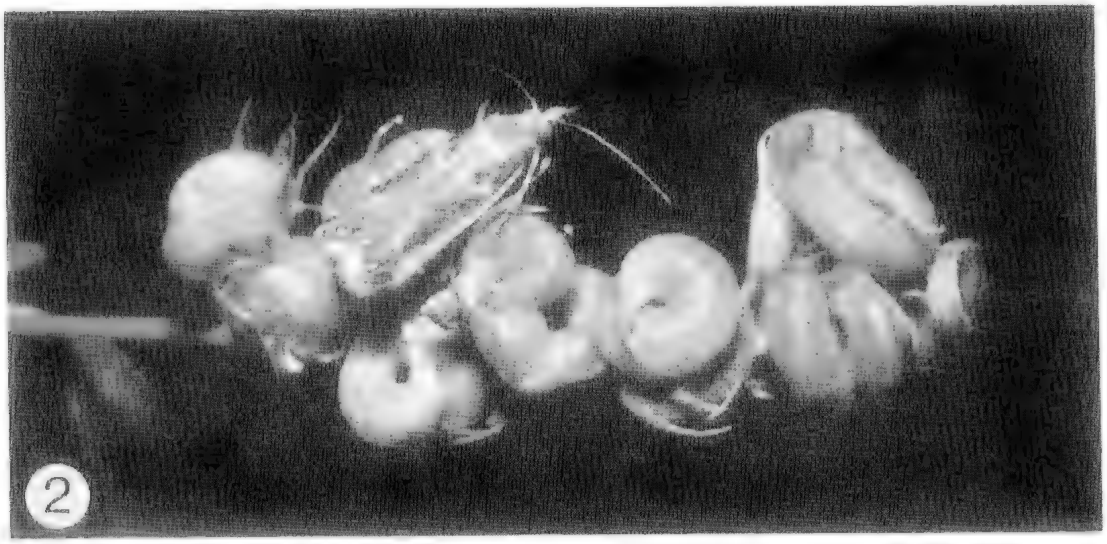

Fig. 2. Female *Etiella behrii* ovipositing onto a raceme of mature green lucerne pods.

forming, on juvenile pods or on mature brown pods. Therefore, in later samples racemes bearing only these stages were excluded from samples, and only racemes bearing some young and mature green pods were examined.

Later in the crop season, when the dryland crop had nearly all brown pods, similar samples were taken from an adjacent crop of irrigated lucerne, of the aphid resistant cultivar WL318, but counts were made of larvae only. Because of possible differences in numbers of larvae in young and in mature green pods, the numbers were expressed as stratified means per 1000 pods.

Rearing techniques and laboratory culture

Techniques for rearing field-collected *E. behrii* larvae through to the adult stage were developed so that a constant supply of each stage was at hand for life-history studies. Small larvae (1st and 2nd instars) collected from lucerne pods were successfully reared on a medium based on either powdered peas or lucerne seed (cf. Shorey & Hale 1965), but the agar had to be boiled for twice the suggested time for the medium to set. Each larva was placed in a 2.5 cm^3 vial containing 1.5 cm^3 of medium. Vials were sealed with hard plastic lids. The pupae were removed from the vials and placed in a dry container until the adults emerged. Both reared and field-collected adults were kept in gauze cages and given access to 10% sucrose solution. All stages were maintained in a dimly lit room held at 24-28°C and 75% R.H. in which the generation time was 25-35 days.

Cooper (1979)[1] obtained large numbers of *E. behrii* eggs from females ovipositing into the crevices of a darkened wooden box. We had no success with this method, nor with a variety of other surfaces including perspex, cardboard, freshly crushed lucerne, and rearing medium with lucerne seeds embedded in it. However, we obtained eggs laid onto freshly shelled peas or fresh mature green lucerne pods. Peas proved most successful because eggs could be easily and safely removed from their smooth surface. Eggs were more difficult to remove from lucerne pods because of their more complex surface. They were collected with a fine paint brush and transferred to a dry glass vial, and the 1st instar larvae were then transferred to a second vial containing rearing medium. With this method we initially obtained 80 eggs and reared 90% through to the adult stage.

Surveys of natural vegetation

Extensive surveys for *E. behrii* larvae were carried out in the native vegetation surrounding the irrigated lucerne growing area south of Keith (for approximately 8 km in each direction) and along road-sides between Tintinara and Willalooka (35 km north-west of Keith) in October-November, 1981. Extensive surveys were also conducted by one of us (DGT) in 1959-60 around Keith and Tintinara, and this information was extracted from the unpublished records of the (then) Department of Entomology, Waite Agricultural Research Institute.

[1]Cooper, D.J. (1979) "The Pathogens of *Heliothis punctigera* Wallengren". Ph.D. thesis, University of Adelaide, Unpubl.

Parasitoids and pathogens of E. behrii

To trap adults of known parasitoids of *E. behrii*, ten yellow pan traps filled with soapy water were placed around the edges of the irrigated WL318 lucerne crop and were examined once per week. The traps were run from early December 1981 to mid-February 1982. In addition, 41 late-stage *E. behrii* larvae (4th and 5th instars) collected from both the dryland and irrigated lucerne crops were reared on artificial diet in the laboratory to check for possible parasitoids. Similarly, one of us (DGT) collected large numbers of *E. behrii* larvae from both native and crop plants in 1959-60 to obtain parasitoids. Also, other workers have bred parasitoids from *E. behrii* collected in the Keith area over the last 40 years. Voucher material of parasitoids collected in the above manner has been lodged in the insect collection at the Waite Institute, and has been used to collate the data presented here.

Pathogens of 16 field-collected 4th and 5th instar larvae that died soon after in the laboratory were screened for pathogens by D.J. Cooper at Waite Institute using the methods of Cooper (1979)[1]

Results and Observations

Life history stages

At all stages of its life cycle *E. behrii* parallels descriptions of both the behaviour and the appearance of *E. zinckenella*, apart from being slightly smaller in size (Abul-Nasr & Awadalla 1957; Stone 1965; Singh & Dhooria 1971). The eggs are ovoid, averaging 0.6 mm in length (S.D. = 0.03; n = 50) and 0.4 mm in width (S.D. = 0.3), colourless when first laid, but soon turn pale yellow or orange. A day before hatching the black head capsules and prothoracic shields of the larvae are clearly visible through the chorion. Eggs are laid on either young or mature green pods, and are usually placed between the pod and the calyx or between the coils of the pod.

The frequency distribution of head capsule widths of field-collected larvae suggested five peaks and hence five instars (Fig. 3), but there was much variation between peaks. The range of each instar was better differentiated by the minima of a three-point moving average process (Fig. 3). The mean widths for five instars were then calculated as 0.18, 0.28, 0.44, 0.70, and 0.99 mm with multipliers between means, for Dyar's law, of 1.54, 1.59, 1.60 and 1.41. Five instars were also confirmed from the rearing of *E. behrii* in the laboratory. The 1st instar has a pale yellow body and a very distinctive black head capsule and prothoracic shield. Soon after hatching it constructs a fine funnel-like silk tube around itself with one end attached to the surface of the pod; it then chews through the pod and into a seed where it remains feeding. The entrance hole in the pod quickly heals over, the web tube soon disintegrates, and no evidence remains to indicate that the pod is infested. The larva does not normally leave this first seed until most of its contents are devoured. It then attacks the next seed in the pod, although it is now too large to get inside it. By the late 3rd to early 4th instar, the larva chews its way out of the original pod and enters one or more new pods, eating some (and occasionally all) of the seeds within. Commonly, at this stage most seeds are only partly devoured. The larva now has a black head capsule, semi-circular prothoracic shield and spiracles. The pro- and mesothorax are golden-brown, the metathorax and abdomen pale green. There are seven dorsal and lateral longitudinal pale golden-brown stripes on the body. By the late 4th instar the larva attacks several pods, meshing these and its frass together with silk to form a protective tent. This webbing is the first readily observed outward sign that *E. behrii* has attacked a crop. By the 5th instar the larva has a pale golden-brown head with dark brown mandibles. The prothoracic shield is still black but the rest of the body is green with a pinkish tinge to the abdomen. The longitudinal bands are more diffuse and pinkish. This final instar becomes a steadily darker pink, the green being masked completely just prior to pupation. Pupation takes place a few centimetres beneath the surface of the soil, inside a cocoon of silk, which incorporates particles of soil.

Adult moths are small (10-15 mm long), greyish and distinctive because of their typical 'snout' (formed by the forward-directed palps), the white stripe along the full length of the leading edge of each fore wing, and the transverse orange band near the base of each fore wing (Fig. 2). At rest, moths have an 'alert' appearance with the head and thorax raised and the abdomen and distal ends of the wings touching the surface. The antennae of the female are smooth and undifferentiated while those of the male have an enlarged basal segment and a 'bush' of scales on the elongated second segment. The maxillary palps of the female diverge at their second joint to form an open 'V' at the tip of the snout. These palps are parallel in the male moth.

Host plants and sources of infestation

Table 1 lists all the plant species for which *E. behrii* larvae have been recorded feeding on their seed in S.A. from 1959 to 1982. Larvae have also been recorded on many of the listed exotic species in other states, as well as on soybean (*Glycine max* (L.) Merrill), peanuts (*Arachis hypogaea* L.) and *Acacia cyclops* A. Cunn. ex G. Don in Western Australia, Northern Territory (Common 1990) and Queensland (Turner 1980). Of all these hosts, lucerne is the most commonly and severely attacked, but the species also causes sporadic damage to lupins, field peas and some clovers (Austin *et al.* 1986; DAM & DGT, unpubl.).

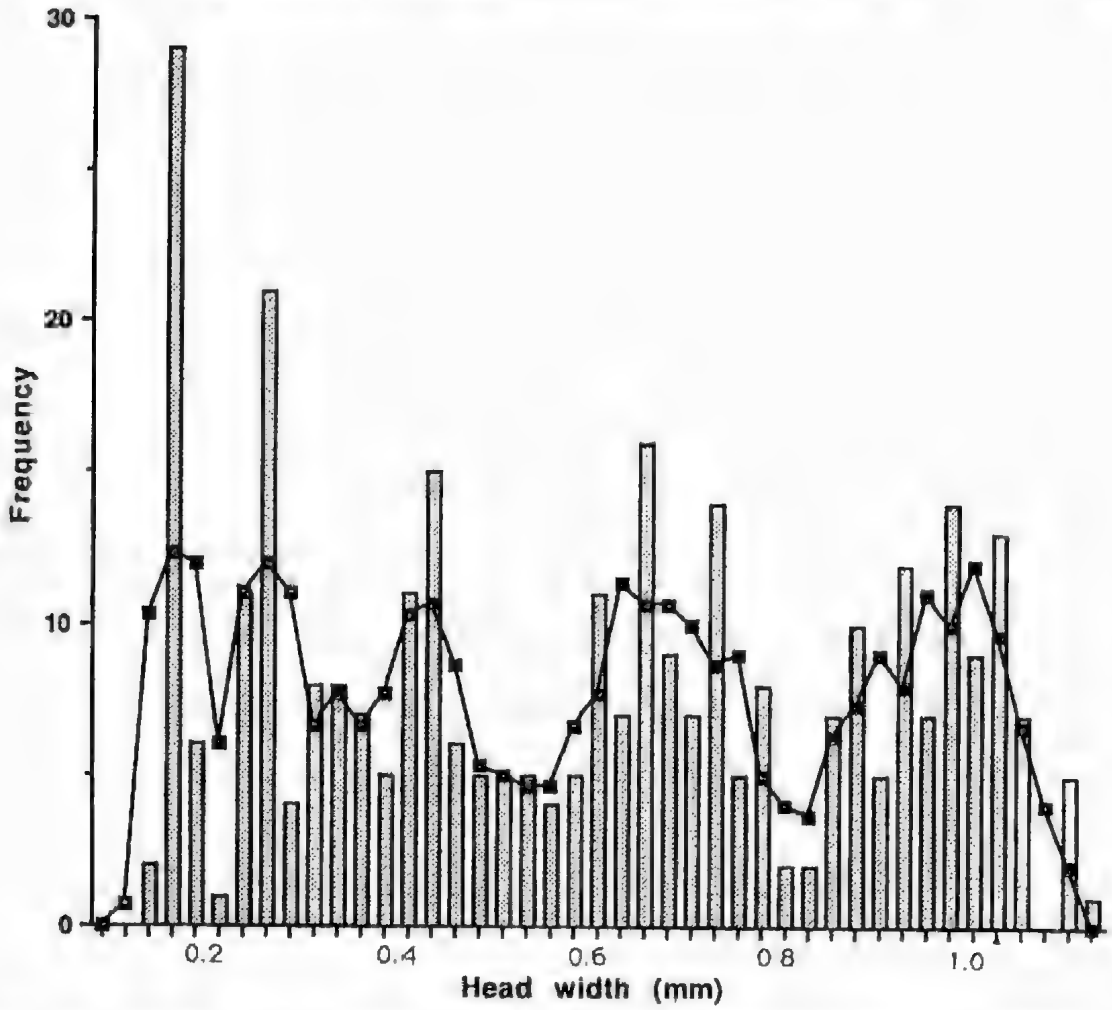

Fig. 3. Head capsule widths of larvae of *Etiella behrii* collected randomly from the field at 'Brecon' (Keith) (n= 329), expressed as a frequency distribution (histogram) and three-point moving averages (■).

The survey of native vegetation in late 1981 revealed that there is very little native scrub left in the Keith area, and what patches do remain are small, considerably disturbed and have very few native legumes, both in numbers of species and individual plants. Far more commonly encountered are volunteer plants of various exotic weed, crop and pasture legumes (especially lucerne) along road-sides, in clearings in scrubland, and in fields carrying other crops such as lupins. Lupins are a potential source of recent significance which have been planted more frequently in the Keith area since 1980. Lupins are planted from early winter to early spring, the seed ripening and drying out up until late November, thus providing an ideal early source of food for larvae, the adults of which emerge early in spring. Samples of 200 pods of green mature lupin pods taken from crops south of Keith and near Tintinara in early November, 1981 showed a small (<1%) infestation of *E. behrii* larvae.

Seasonal phenology

Observations in the laboratory indicate that females can lay more than 200 eggs and that eggs hatch within 24 h at 30-35 °C, but usually hatch after 4-7 days in the field in spring-summer. Larval duration in the field during spring-summer varied from 10-28 days and the pupal period from 14-21 days. Adults survived 7-21 weeks in the laboratory when held at ambient temperature and supplied with 10% sucrose solution.

The light-trap catches of adults at the Waite Institute campus in 14 day intervals for the period 1.iii.1959 to 18.ii.1960 are given in Fig. 4. These catches suggest

TABLE 1. *Known host plants of* Etiella behrii *in South Australia (records collected 1959-82).*

Native Legumes

Acacia victoriae Benth (elegant wattle)
Daviesia brevifolia Lindley (leafless bitter-pea)
Eutaxia microphylla (R. Br.) Black (Eutaxia, mallee bush-pea)
Hardenbergia violacea (Schnee.) Stearn (native lilac)
Pultenaea tenuifolia R. Br. ex Sims
Pultenaea densifolia F. Muell. (dense-leaved bush-pea)

Introduced Legumes

Cytisus scoparius (L.) Link (English broom)
Cytisus proliferus L.f. (tree lucerne)
Genista monspessulana (L.) L. Johnson (Montpellier broom)
Lupinus cosentinii Guss. (Western Australian blue lupin)
Lupinus angustifolius L. (lupin)
Lupinus uliginosus Schkyhr (birdfoot trefoil, greater lotus)
Medicago ciliaris (L.) Krocker
Medicago littoralis Rohde ex. Lois (strand medic)
Medicago polymorpha L. var. *polymorpha* (burr medic)
Medicago rugosa Desr. (gamma medic)
Medicago sativa L. (lucerne, alfalfa)
Medicago truncatula Gaertner (barrel medic, snail medic, caltrop medic)
Pisum sativum L. (field peas)
Trifolium fragiferum L. (strawberry clover)
Trifolium resupinatum L. (shaftal clover)
Trifolium subterraneum L. (subterranean clover)
Vicia dasycarpa Ten. (woolly-pod vetch)
Vicia villosa Roth. (hairy vetch, winter vetch)

at least four overlapping generations each year, with peak catches in late September (spring), late November and late December. There is then a generation with a peak in mid to late February and a hint of other small generations in March-May. Our trap catches for adults in December 1981 to January 1982 for the Keith area are in accordance with these earlier data by clearly detecting two large summer peaks (Fig. 6), even though they occurred at a slightly later time than the 1959-60 peaks. When related to monthly mean temperatures (Anon. 1987) by iterative calculations, these observations suggest a mean generation time of about 210 day degrees above about 13°C.

South Australia has a hot dry summer (Anon. 1987) and as summer progresses, dryland lucerne should gradually becomes unfavourable for *E. behrii*. Our survey in dryland lucerne in the early summer of 1981-82 was planned to quantify this change; and in

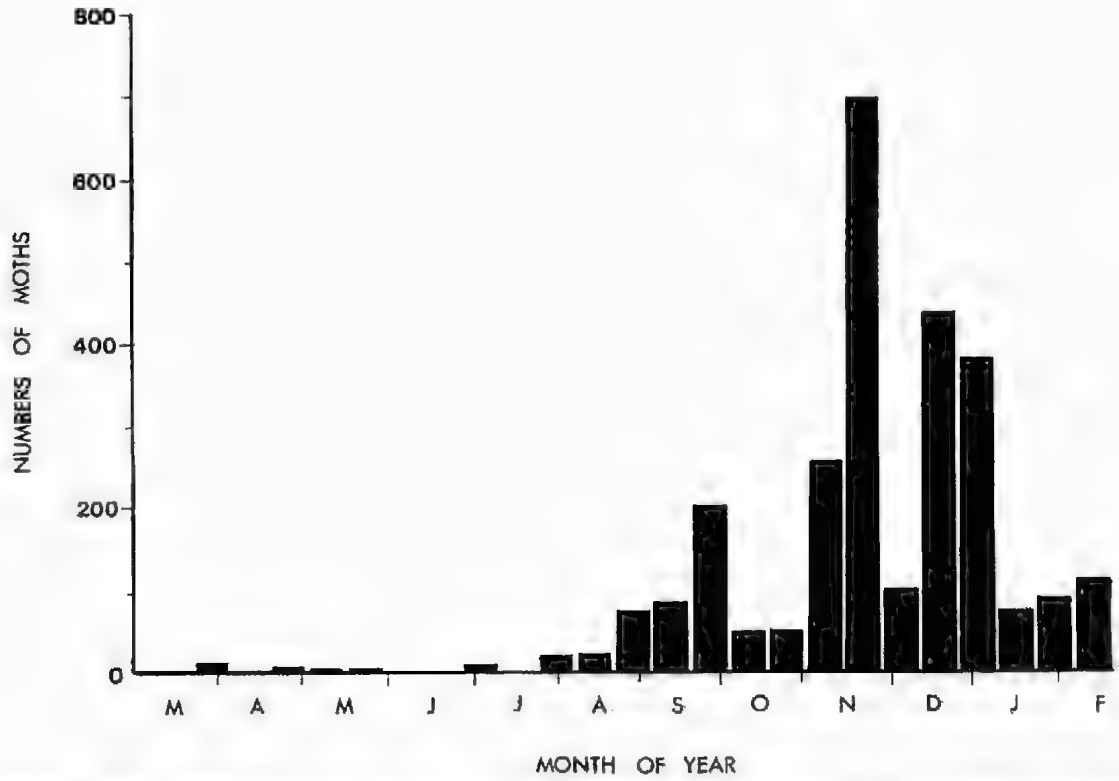

Fig. 4. Light-trap catches of adult *Etiella behrii* at the Waite Institute campus, Adelaide in 1959-60 accumulated in intervals of 14 days.

Table 2 are given, for each sample (a) the numbers of juvenile, young and mature green pods , and (b) the total number of eggs and larvae of *E. behrii* in young and mature green pods (none were found in juvenile pods).

The total numbers of *E. behrii* were obviously greater in mature green pods than in young ones from 6.i.82 onwards (Table 2), but the numbers of different stages were too small to allow comparisons between the two sorts of pods, except for eggs and 1st+2nd instars on 30.xii.81 and 6.i.82. For eggs on 30.xii.81 plus 6.i.82, there was a significantly greater number on young pods (51 on 1250 pods) than on mature green pods (31 on 1211 pods) ($\chi^2 = 3.95$, $p < 0.05$). For eggs plus 1st and 2nd instars, 78 on 1250 young pods were also significantly more frequent than 47 on 1211 mature green pods ($\chi^2 = 7.69$; $p < 0.01$). The comparison of these two sets of data suggest that in the samples for these two days some young larvae were failing to establish in the mature green pods. Obviously the larger number of all stages of *E. behrii* on mature green pods after 6.i.82 was therefore due to larger numbers of older larvae. Because the two types of pods could be considered as different sampling strata, the total numbers of *E. behrii* in each sample were subsequently expressed as means per 1000 pods, corrected for the different numbers of young and mature pods. Such means of all stages of *E. behrii* are also given in Table 2, and separate means for eggs and for instars 1+2, 3+4 and 5 are given in Fig. 5.

In Table 2, the decline with time of the numbers of both juvenile and young pods illustrates the maturation of the crop, and the data in Table 2 and Fig. 5 indicate a concomitant decrease in numbers of eggs and 1st + 2nd instars of *E. behrii* and an increase in numbers of older larvae. To try to make more sense of these trends, the numbers of eggs and of all larvae were plotted against the numbers of adults of *E. behrii* caught per week at the light trap at Keith (Fig. 6). The data suggest that the numbers of eggs laid up to and after the first peak of moths were strongly correlated with the numbers of moths each week. However, the

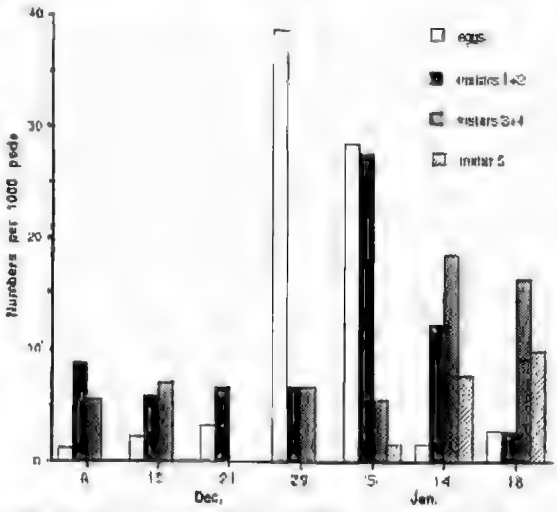

Fig. 5. Corrected numbers per 1000 pods of *Etiella behrii* eggs, 1st + 2nd instar, 3rd + 4th instar, and 5th instar larvae in a dryland lucerne crop at 'Brecon' (Keith) in relation to calendar time from 1.xii.1981.

numbers of eggs on 15.i.82 and 19.i.82 were much lower than expected in relation to the number of moths, which had increased to a second peak (Fig. 6). Unfortunately, no counts of eggs were made after 19.i.82 because attention was then diverted to the main irrigated seed crop which was in full flower.

The cause of the decline in numbers of eggs in the dryland crop on 15.i.82 and 19.i.82 (Figs 5, 6) is not known. There seemed to be an abundance of suitable pods for oviposition on these two dates (Table 2), but it is possible that the crop had dried out further so that even the young pods were subtly different from those on earlier dates and were unsuitable for oviposition. So too there was an unexpected decrease in the numbers of young larvae on 19.i.82 (Fig. 5), possibly again because the pods were not as suitable for their establishment as they had been earlier.

The numbers of larvae in irrigated lucerne seed crops were of particular interest to us from the view point

TABLE 2. *The numbers of juvenile (J) , young (Y) and mature green (M) pods in each sample; and the numbers of all stages of* E. behrii (E.b.) *in each category of pods.*

Date of sample	Numbers of pods			Numbers of *E.b.* in		Mean *E.b.* per
	J	Y	M	Y pods	M pods	1000 Y+M pods
09.12.81	276	804	91	10	4	15.6
16.12.81	362	637	207	7	6	15.4
22.12.81	267	573	330	6	3	10.0
30.12.81	113	650	542	30	33	52.9
06.01.82	95	600	669	21	57	61.5
15.01.82	17	187	463	2	24	40.0
19.01.82	15	238	1165	1	44	32.1
Total	1145	3689	3467	77	171	

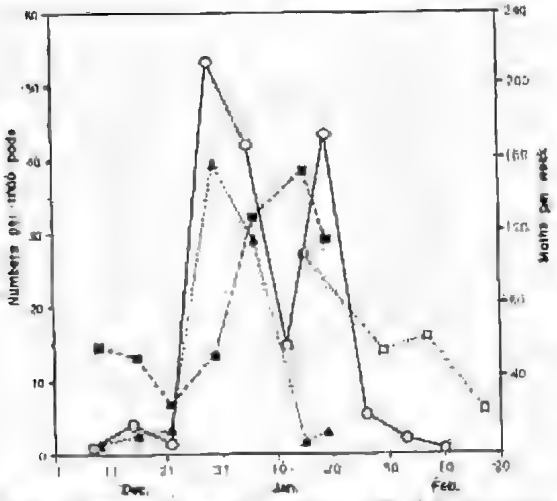

Fig. 6. Number of eggs (▲) and larvae (■) of *Etiella behrii* per 1000 pods in samples taken at 'Brecon' (Keith) in a dryland lucerne crop in the summer of 1981-82; the number of larvae (□) similarly sampled in an adjacent irrigated lucerne crop; and the number of moths (○) caught weekly in a light-trap in the same irrigated crop, in relation to calendar time from 1.xii.1981.

of pest management, and the irrigated and unsprayed WL318 crop, which we sampled later in the season, had been managed so that it flowered later than the adjacent dryland crop; and on 19.i.82 it was at about the same stage of development as the dryland crop had been on 9.xii.82. The numbers of larvae in the irrigated crop are also given in Fig. 6. On 15.i.82, they were about the same as those in the dryland crop on 15.i.82 and 19.i.82, but they similarly declined thereafter (Fig. 6) despite an abundance of seemingly suitable young and mature green pods for *E. behrii*. In particular, there was no increase in the numbers of larvae after the second peak of trapped moths on 19.i.82. Unfortunately, eggs were not recorded in these samples from the irrigated lucerne, nor were the larvae categorised into instars. It is not known, therefore, where the mortality occurred that caused the decreasing trend in larval numbers. The weather was not obviously unfavourable for moth survival and oviposition, so the mortality is likely to have been at the egg and/or larval stage. Two main possibilities may be suggested for this decline. Firstly, it is possible that there was a very low establishment of young larvae on the aphid resistant cultivar WL318, as Perrin (1978), for example, found in some varieties of cowpea attacked by *Cydia ptychora* (Meyrick). The second possibility is that the mortality was due to predators and pathogens. In particular, the decrease in larval numbers occurred at the same time as a dramatic increase in the numbers of *Campylomma livida* Reuter (dimpling bug), which is thought to be partly predacious, as is *C. verbasci* (Meyer), a well-known predator of mites, aphids and psyllids in Canada (McMullen & Jong 1970).

Finally, the second peak of moths in mid-January (Fig. 6) may be expected to be smaller than the first one because the area of dryland lucerne is much greater than that of irrigated lucerne and, as summer progresses, dryland lucerne is no longer favourable for *E. behrii*. So one might therefore expect fewer moths to be caught in a light-trap in February-March, as is partly illustrated in Fig. 6 for Keith. Other crops attacked by *E. behrii*, such as lupins, would similarly cease to produce suitable green pods for young caterpillars in mid January unless they were irrigated. Therefore, in most localities there would be a reduction in numbers of larvae in late January to early February and a subsequent reduction in the numbers of moths at the next peak catch of moths, as shown in Fig. 4 for Adelaide in mid to late February. The few moths flying in late February would find even fewer suitable pods for oviposition at the end of the hot dry summer. So the species is likely to be relatively rare in most localities after February and until the next flush of plant growth in spring, following winter rains. During this interval the species could either enter an obligate diapause or it could continue to breed in reduced numbers (on volunteer lucerne). The light-trap data for Adelaide (Fig. 4) strongly support the latter alternative, because a few moths were caught in late April to early May. The lack of a diapause was also demonstrated directly by one of us (DGT) by successfully incubating to adult emergence, larvae collected over the winter of 1959.

Parasitoids, predators and pathogens

The parasitoid species which have been recorded from *E. behrii* are given in Table 3 along with the stage from which they emerge, whether they are solitary or gregarious, and their status as either primary or hyperparasitoids. The ichneumonid *Temelucha cycnea* Kerrich and the braconid *Iconella alfalfae* (Nixon) have been recorded as causing between 2% and 11% mortality to field populations in the Keith area in 1959-60 (DGT unpubl.), while the other species listed have been only rarely encountered. Yellow pan-traps placed in the field at 'Brecon' in early December 1982 first caught *T. cycnea* in early February. The numbers of this parasitoid appeared to increase through February and March, but there were too few collected per trap to quantify differences between samples. *Phanerotoma* sp. was also caught in late February but in very low numbers.

Of 41 larvae of *E. behrii* taken from the field in late January to screen for parasitoids, 25 pupated, and three were parasitised (two by *T. cycnea* and one by *Panerotoma* sp.). *T. cycnea* oviposits into early stage larvae after the latter emerge from the pod and begin

to build a webbed retreat, while *Panerotoma* sp. oviposits into the eggs of its host. Both species then complete their development after the final host instar has dropped to the soil and pupated. During the 1981-82 study we did not record any other parasitoid species, even though *I. alfalfae* has been recovered in moderate numbers in the past (DGT unpubl.).

We did not directly observe any predation upon eggs and larvae of *E. behrii*, but several general predators were seen in lucerne crops, and they may feed on *E. behrii*. The predators included *C. livida* (see above) and spiders, particularly of the families Oxyopidae, Araneidae, Lycosidae and Thomisidae. Of these species *C. livida* was by far the most common in irrigated crops during January-February 1982.

Sixteen of the 41 screened larvae died before they pupated. After death they became soft, darker in colour and developed faint spots under the integument. These larvae were later examined and found to contain large numbers of microsporidian spores and some bacteria (*Bacillus* sp. — possibly *B. thuringiensis* Berlinger) in the haemolymph. Nothing is known of the mortality caused by these pathogens in the field, but *B. thuringiensis* at least is known to be highly toxic to *E. behrii* larvae in the laboratory, having an LC_{50} value of 311 spores/mm^3, a figure 20 times lower than that for *Helicoverpa armigera* (Hübner) (Cooper 1983).

Discussion

Irrigated lucerne crops flower and form pods later than dryland lucerne and volunteer plants which grow around irrigated crops, along road-sides and in scrubland. So the number of moths available to attack irrigated lucerne crops each year should depend on the number and suitability of pods available to the earlier generations of *E. behrii* in that season, and on some function of weather. However, the very low numbers of larvae in the irrigated crop south of Keith in January-February 1982, despite the presence of a large number of adult moths in the vicinity (Fig. 6) and suitable oviposition sites, suggests that some variable or variables, other than the number of moths, may be a key factor in the amount of crop damage that occurs from year to year. This variable might be predation or parasitism on eggs and young larvae, the effect of pathogens, or some property of the plant which prevents young larvae establishing and surviving in pods, either of certain cultivars or in certain years. Such a variable might also account for the unpredictability of attack of lucerne by *E. behrii*. In most years damage is so slight as to go unnoticed, but occasionally there is a very heavy infestation in one season. Such outbreak seasons appear from the available records to be infrequent, but when they do occur, outbreaks are widespread. To date, further research aimed at examining the factors responsible for heavy infestations of *E. behrii* in seed lucerne crops in South Australia, has been hindered by the infrequency of such events. In recent years there have been only low or moderate numbers of this pyralid pest reported in seed crops in the Keith area, possibly because of the more widespread and effective use of pesticides since the early 1980's.

TABLE 3. *Parasitoids known to attack various stages of* Etiella behrii *in South Australia (records collected 1959-82).*

Parasitoid species	Stage from which parasitoid emerges	Primary (P) or hyperparasitoid (H) solitary (S) or gregarious (G)
Ichneumonidae		
Temelucha cycnea Kerrich	pupa	P;S
Enytus sp.	?	P;S
Braconidae		
Iconella alfalfae (Nixon)	5th instar larva	P;S
Phanerotoma sp.	pupa	P;S
Bassus sp. 1	5th instar larva	P;S
Bassus sp. 2	5th instar larva	P;S
Bracon sp.	mature larva	P;S
Elasmidae		
Elasmus sp.	pupa	H;S or G
Eurytomidae		
Eurytoma sp.	pupa	P;S
Tachinidae		
2 Siphonini (gen. & sp. indet.)	mature larva	P;S

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We wish to thank Mr A. Campbell for access to his property, 'Brecon', Dr David Cooper for assaying pathogens of *Etiella*, Dr Jenny Gardner for identification of native plants, and Drs Brian Cantrell and Mike Sharkey for identification of dipteran and hymenopteran parasitoids, respectively. We gratefully acknowledge the Commonwealth Special Research Grants Scheme and the lucerne seed growers through the Seed Section of the United Farmers and Stock Owners of South Australia Inc. for funding this project. We also thank Paul Dangerfield for providing technical assistance in the preparation of the manuscript.

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INCABATES HAMMER AND SETINCABATES GEN. NOV. (ACARIDA: CRYPTOSTIGMATA: HAPLOZETIDAE) FROM SOUTH AUSTRALIAN SOILS

*BY D. C. LEE**

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Incubates Hammer is commented on and an allied genus, *Setincabates* gen. nov., established. Three new species are described from South Australian soils: *I. macronudus* sp. nov., *I. punctatus* sp. nov. and *S. hypersetosus* sp. nov. (type). *I. angustus* Hammer, previously known from New Zealand, is newly recorded from Australia and *I. medius* Hammer is newly regarded as its junior synonym. A key is given for the adults of these four species. This is the first record of *Incubates* from Australia. An African species previously grouped in *Incabates* is newly combined as *Muliercula longisaccula* (Mahunka).

KEY WORDS: *Incabates angustus* Hammer, *Incabates macronudus* sp. nov., *Incabates punctatus* sp. nov., *Setincabates hypersetosus* gen. nov., sp. nov., Haplozetidae, Acarida, soils, South Australia.

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Introduction

The genus *Incabates* Hammer, 1961 and a similar undescribed genus are examined as part of an ongoing study of sarcoptiform mites sampled from nine florally diverse South Australian sites, and for which Lee (1987) provided an introduction to the relevant work on the advanced oribate mites. The relevant mites are from soil and plant litter or moss under either savannah woodland, sclerophyll forest, mallee or coastal vegetation at only four of the sites.

Incabates is grouped in Haplozetidae Grandjean, 1936, which has been discussed by Lee & Shepherd (1990) in considering *Magnobates* Hammer, 1967. Relationships between *Incabates*, the new genus and some other haplozetid genera are discussed. *I. angustus* Hammer, 1967 is newly recorded from Australia, and two new species of *Incabates* and the new genus together with one new species are described.

Material and Methods

New material examined here, collected by the author, is deposited mostly in the South Australian Museum (SAMA), but also in the Natural History Museum, London (BMNH), the Field Museum, Chicago (FMNH) and the New Zealand Arthropod Collection, Land Care Research, Auckland (NZAC), whilst previously described material is deposited in the Zoological Museum, Copenhagen (ZMC). The morphological notational system follows Lee (1987), the somal chaetotaxy of which is summarised in Figs 2 and 3, with the total setae present in each file (e.g. 6Z) indicated by number coming first, whilst a particular seta (e.g. Z6) would have the number last. The venter and legs have been described only for *Incabates punctatus* because of their uniformity within the genus. The abbreviations for zoogeographical regions follow Lee (1970, Fig. 427). Descriptions of eggs are based on those still within the female soma. All material was examined using a Nomarski interference contrast device. All measurements are in micrometres (μm) and were made using an eyepiece micrometer at ×250 magnification.

Key to Australian *Incabates* and *Setincabates* species (adults)

1. Thirteen pairs of hysteronotal seta. Hysteronotal foramen *F3* sacculate without narrow duct .... *Setincabates hypersetosus* sp. nov.
   Ten pairs of hysteronotal seta or alveoli. Hysteronotal foramen *F3* sacculate with narrow duct ..... *Incabates*. 2
2. Hysteronotal setae represented only by alveoli. Tutorium absent ..... *I. macronudus* sp. nov.
   At least one pair of hysteronotal setae present. Tutorium present 3
3. Six posterior small hysteronotal setal pair present (*J5*, *J6*; *Z5*, *Z6*; *S5*, *S6*). Anterior soma punctate ..... *I. punctatus* sp. nov.
   One posterior small hysteronotal setal pair present (*J6*). Anterior soma not punctate ..... *I. angustus* Hammer.

Systematics

Incabates Hammer

Incabates Hammer, 1961, p. 108 (type species by monotypy: *Incabates nudus* Hammer, 1961); Coetzer, 1968, p. 25; Balogh & Balogh, 1984, p. 274; Luxton, 1985, p. 67; Corpuz-Raros, 1980; 174.

* South Australian Museum, North Terrace, Adelaide, S. Aust. 5000.

Definition: Haplozetidae. Hysteronotum with 10 pairs (2*J*, 6*Z*, 2*S*) of short setae, microsetae or alveoli without their setae. Hysteronotal foramina with saccule bag-like, either tapering gradually to pore or with short narrow duct near pore. Dorsosejugal furrow entire. Translamella and prelamella absent, costate or lineate tutorium (between setae *j*1-*z*2) sometimes present. Rostral seta (*j*1) directly in front of lamellar seta (*z*1). Pteromorph movable, with clear weakly sclerotized basal line. Discidium triangulate. Tibia I with large solenidium (*ω*2) on tubercle. Tibia II without distodorsal spur. Genu I and II with two setae (*v* absent). Trochanter IV usually with distodorsal process extended over femur IV (exception: *Incabates augustus*), distodorsal crown with only anterior angulate lobe, broad flange extending along entire venter of caput. Pretarsus with three claws, slimmer lateral claws with pointed tip.

General Morphology of Australian species: Somal length range for adults: 239-445 (for all species 239-496). Somal chaetotaxy: 2*j*, 2*z*, 1*s*; 2*J*, 6*Z*, 2*S*; 3*I*, 1*II*, 3*III*, 3*IV*; 4*Zg*, 1*Sg*; 2*JZa*, 3*Sa*. Leg chaetotaxy (solenidia in parentheses): I – 1, 5, 2(1), 4(2), 20(2); II – 1, 5, 2(1), 4(1), 16(2); III – 2, 3, 1(1), 3(1), 15; IV – 1, 2, 2, 3(1), 12. Alveoli of somal setae bounded by refractile ring, canal short and tapering without internal refractile ring. Pteromorph may lie close to pleural surface or be lifted away from it. Sub-bothridial flange present. Apodemes I, II, ventrosejugal and III present. Ventrosejugal gap not wider than genital orifice. Subpedal and circumpedal ridges merged into single continuous line. Slit-like pore *Saf* nearly longitudinal (less than 45° from longitudinal axis). Proximoventral spur on femur I without caput collar. Conspicuous ventral flanges on femora II, III, and IV, on femur II margin curved, not angulate.

Distribution: Peru (NTc), Japan (Pc), Philippines (Om), Australia (Aa), New Zealand (An), Fiji (Ap). All species from outside South Australia are from moist localities, often in moss, either in high altitude grassland or in forest or mangroves, and are sometimes arboreal. In South Australia all three species were collected from the sclerophyll forest site, which has the highest rainfall (annual mean in the range of 1150-1200 mm, mostly in winter), but *Incabates punctatus* sp. nov. was also collected from the two mallee sites which are dry (mean annual rainfall in the range of 350-500 mm).

Remarks: *Incabates* was considered allied to *Protoribates* Berlese, 1908 when it was established. More recently it has been allied to *Scheloribates* Berlese, 1908 (Corpuz-Raros 1980; Luxton 1985), to which it is similar in having a triangulate discidium, hysteronotal sacculate foramina that gradually taper to a pore, and, for some species, in having no tutorium (in species with a tutorium, it only costate). In contrast, *Incabates* has a derived character state, a hinged rather than a fixed pteromorph as in scheloribatid genera, on the basis of which, Coetzer (1968) suggested that *Incabates* should be transferred to the Haplozetidae Grandjean, 1936. Because *Incabates* also has a derived trochanter IV (the distoventral crown with only an anterior lobe that extends along entire venter of caput), and if there is a lateral proteronotal ridge it is a tutorium rather than a prelamella ridge, this grouping in the Haplozetidae is followed here.

In current classifications of the Oripodoidea, the Haplozetidae are not closely allied to the Protoribatidae Balogh & Balogh, 1984, because of the importance given to the former family having derived sacculate hysteronotal foramina, rather than multiporose foramina; but both *Incabates* and *Protoribates* have derived hinged pteromorphs. The significance of particular character states and so the accepted relationships amongst oripodoid taxa, may well change considerably. In this paper it is considered that, since *Incabates* shares some character states with most genera of the more primitive Scheloribatidae Grandjean, 1933, character states that are derived in many members of the Haplozetidae (the discidium is rectangulate, the tutorium is conspicuously laminate and hysteronotal sacculate foramina often have narrow ducts leading to their pores), it is more primitive than *Magnobates* Hammer, 1967 and the genera closely allied to it (Lee & Shepherd 1990).

In distinguishing *Incabates* from other genera, the following scheloribatid genera must be considered: *Muliercula* Coetzer, 1968, *Nanzerlia* Coetzer, 1968 and *Styloribates* Jacot, 1934. These three genera can be regarded as derived within the Scheloribatidae because of character states of the proteronotum and trochanter IV. In general, members of the Scheloribatidae fold leg I against the soma so that the tarsus points downwards behind seta *j*1, lying behind the prelamella ridge, also trochanter IV is simple, with the crown confined to the distal end. In contrast, haplozetids and the three scheloribatid genera listed above, have a tutorium or subtutorium rather than a complete prelamella and, when the leg is folded, tarsus I can point forward between setae *z*1-*j*1, whilst on trochanter IV, the crown extends as a broad flange along the entire venter of the caput. Therefore, these three scheloribatid genera are only distinguished from the haplozetid *Incabates* by having fixed pteromorphs, which is sometimes a difficult character state to assess. Further studies may require that these four genera are either grouped into a new family or that the Scheloribatidae and Haplozetidae are merged.

The naming of a species, that is very similar to the type species of *Muliercula*, as ?*Incabates longisaccatus* illustrates this confusion. It is here combined as *Muliercula longisaccula* (Mahunka, 1984) comb. nov., despite its lack of a tutorium and the presence of a partial prelamellar. This is partly because these

character states are variable in *Incabates*, and therefore the presence of a tutorium may not be diagnostic of *Muliercula*, but it is mainly because the pteromorph is only partially delineated from the hysteronotum by a clear furrow as described for *Muliercula*, where it is regarded as fixed, although ambiguously described by Coetzer (1968) as "pteromorphae immovably hinged". Because of the similarity between *Incabates* and *Muliercula*, despite their grouping in separate families, only the more extensive wing-like expansions of the lamellae of *M. longisaccula* and its occurrence in Africa support the new grouping.

In comparison to other haplozetid genera such as *Haplozetes* Willmann, 1935 and *Magnobates* Hammer, 1967, *Incabates* is regarded as primitive in having a triangulate discidium, as on oribatulid and scheloribatid adults. Similarly it has only two setae on genu I and the alveolar canal of the somal setae is short and simple.

Incabates includes seven species: *I. angustus* Hammer, 1967 (= *I. medius* Hammer, 1971, syn. nov.) from Australia (Aa), New Zealand (An) and Fiji (Ap); *I. macronudus* sp. nov. from Australia (Aa); *I. major* Aoki, 1970 from Japan (Pc); *I. nudus* Hammer, 1961 from Peru (NTc) and Philippines (Om); *I. pahabaeus* Corpuz-Raros, 1980, from Philippines (Om); *I. punctatus* sp. nov. from Australia (Aa); *I. striatus* Corpuz-Raros, 1980, from Philippines (Om).

Incabates angustus Hammer

Incabates angustus Hammer, 1967, p. 43, 44, Fig. 57, 57a.
Incabates medius Hammer, 1971, p. 42, Fig. 49, 49a, syn. nov.

Type material examined: *I. angustus*, lectotype ♀ (labelled "type" in vial of alcohol, three specimens recorded in original description) examined (ZMC), liverworts and small ferns, dead tree trunk, native forest, Waitakere National Park, North Island, New Zealand, M. Hammer, 1962. *I. medius*, lectotype ♀ (labelled type in vial of alcohol, two specimens recorded in original description) examined (ZMC), withered leaves, river bank, above mangroves, Corolevu, Vita Levu, Fiji Islands, M. Hammer, 1962.

Female: Soma oval, brown. Idiosomal length (original description from New Zealand: 'about 0.35 mm', from Fiji: 'about 0.305 mm'), 335 (n = 1, New Zealand) or 318 (n = 25, Sclerophyll forest, 306-332). Leg lengths (femur-tarsus, Sclerophyll forest, for 320): I-142, II-127, III-108, IV-137. Tibial maximum heights (for 320): I-22, II-17, III-14, IV-14.

Proteronotum with medium width rostrum. Integument smooth. Tutorium present, sometimes indistinct level with lamellar seta (*zl*). Sensory seta (*z2*) with globular caput longer than exposed stalk. Subbothridial flange inconspicuous. Posterior margin of bothridium raised to form tooth-like spur. Interlamellar seta (*j2*) longer than distance *j2* - *zl*. Hysteronotum with only one pair (*J6*) of noticeable small setae, nine pairs (*J5*, *Z1-6*, *S5* and 6) of alveoli, possibly with small microsetae. Alveolus *S5* posterior to *Z5* (South Australian specimens) or anterior to *Z5* (New Zealand specimens). Foramen *F3* conspicuously larger and sometimes sacculus bilobed (South Australian specimens) or slightly larger, not bilobed (New Zealand specimens).

Idiosternal setae fine and short, coxite seta *I3*, *III3* and *IV3* (not illustrated as present by Hammer, 1967: Fig. 57a) longest. Integument smooth except for indistinct reticulations around ventrosejugal apodeme and apodeme III. Discidium height less than 0.5× height of pedotectum II, coxite seta *IV3* near discidium base. Eggs subellipsoidal, exochorion smooth, mean size 151 × 72 (n = 7), length 48% of somal length, eggs per female = 1 (n = 3), or 2 (n = 2).

Legs short (median femur-tarsus length: 40% of somal length) with stout girth (mean maximum tibial height 50% of mean length). Trochanter IV anterior margin parallels posterior margin of femur IV caput, angulate distodorsally but without process extended over femur IV.

Male: Similar to female but idiosoma shorter, mean length, 293 (7, Sclerophyll forest, 283-303) or 319 (1, Savannah woodland)

Referred material: 12 females (SAMA N19911 — N199112), seven males (SAMA N199113 — N199119), plant litter, sparse moss and sandy soil, under sclerophyllous shrub amongst messmate stringybark (*Eucalyptus obliqua*), dry sclerophyll forest, near summit of Mt Lofty (34°59'S, 138°45'E), Cleland Conservation Park, 9.v.1974.

One male (SAMA N199120), grass, moss, plant litter and loamy soil, under manna gum trees (*Eucalyptus viminalis*), savannah woodland, Chambers Gully (34°58'S, 138°41'E), Cleland Conservation Park, 12.vi.1974.

Remarks: Incabates angustus was one of four species that have only a single pair of hysteronotal seta (*J6*), but one of the other three species, *I. medius* from Fiji, is here synonymised with it. The other two species, *I. striatus* with a striated integument and the stouter *I. nudus* with a much broader lamella, are easily distinguishable as separate species. The slim *I. angustus* and *I. medius* are very similar with the new material from South Australia having intermediate character states. *I. angustus* is 350 μm long, has hysteronotal seta *S6* anterior to *S5* and the interlamellar seta (*j2*) is about 0.75× the length of the lamellar seta (*zl*). *I. medius* is 305 μm long, has hysteronotal seta *S6* level with *S5* and the interlamellar seta is about 0.5× the length of the lamellar seta. The specimens from South Australia are similar in size to *I. medius*, have seta *S6* posterior to *S5*, and the relative sizes of the interlamellar and lamellar setae are as *I. angustus*.

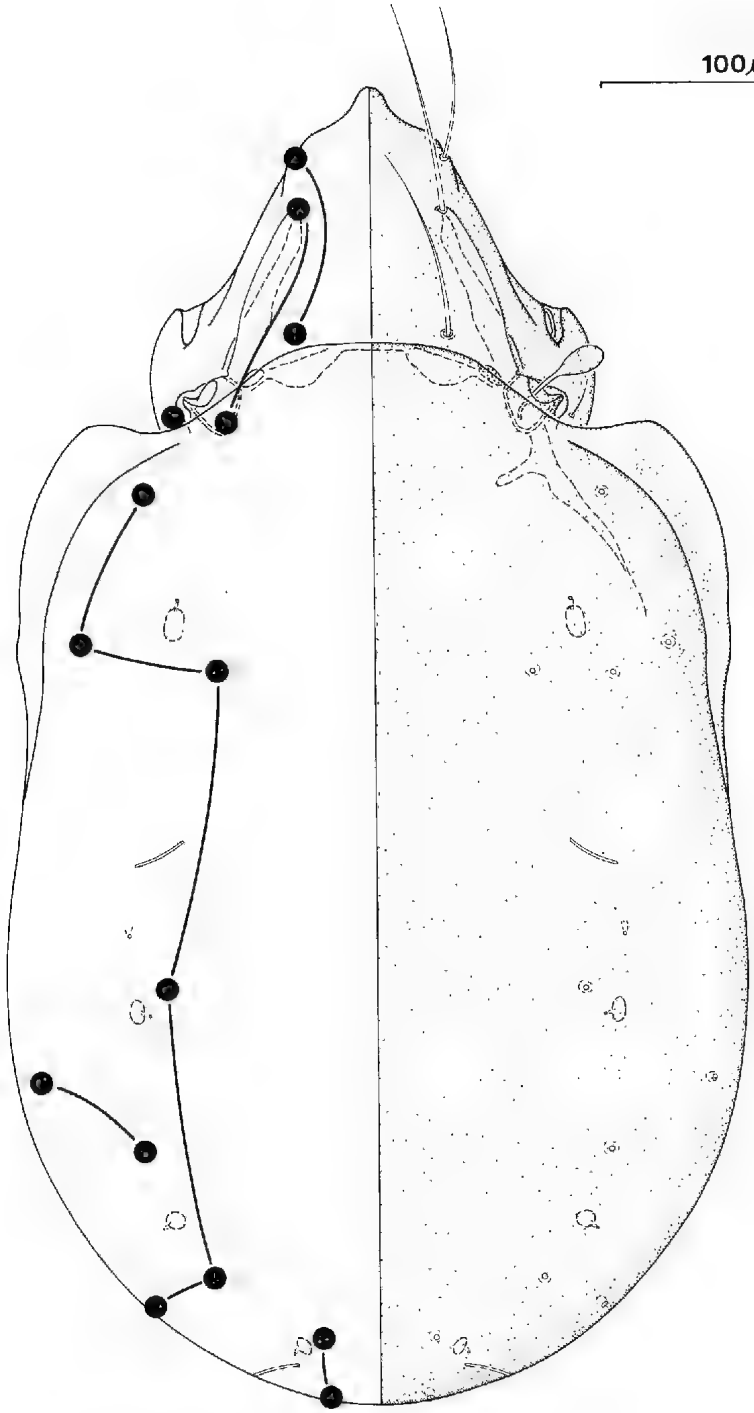


Fig. 1. *Incabates macronudus* sp. nov., female soma, notum.

These differences are here regarded as intraspecific variations within a species distributed across Australia, New Zealand and Fiji, and comparable with differences within *I. nudus* from Peru and the Philippines (Corpus-Raros 1980).

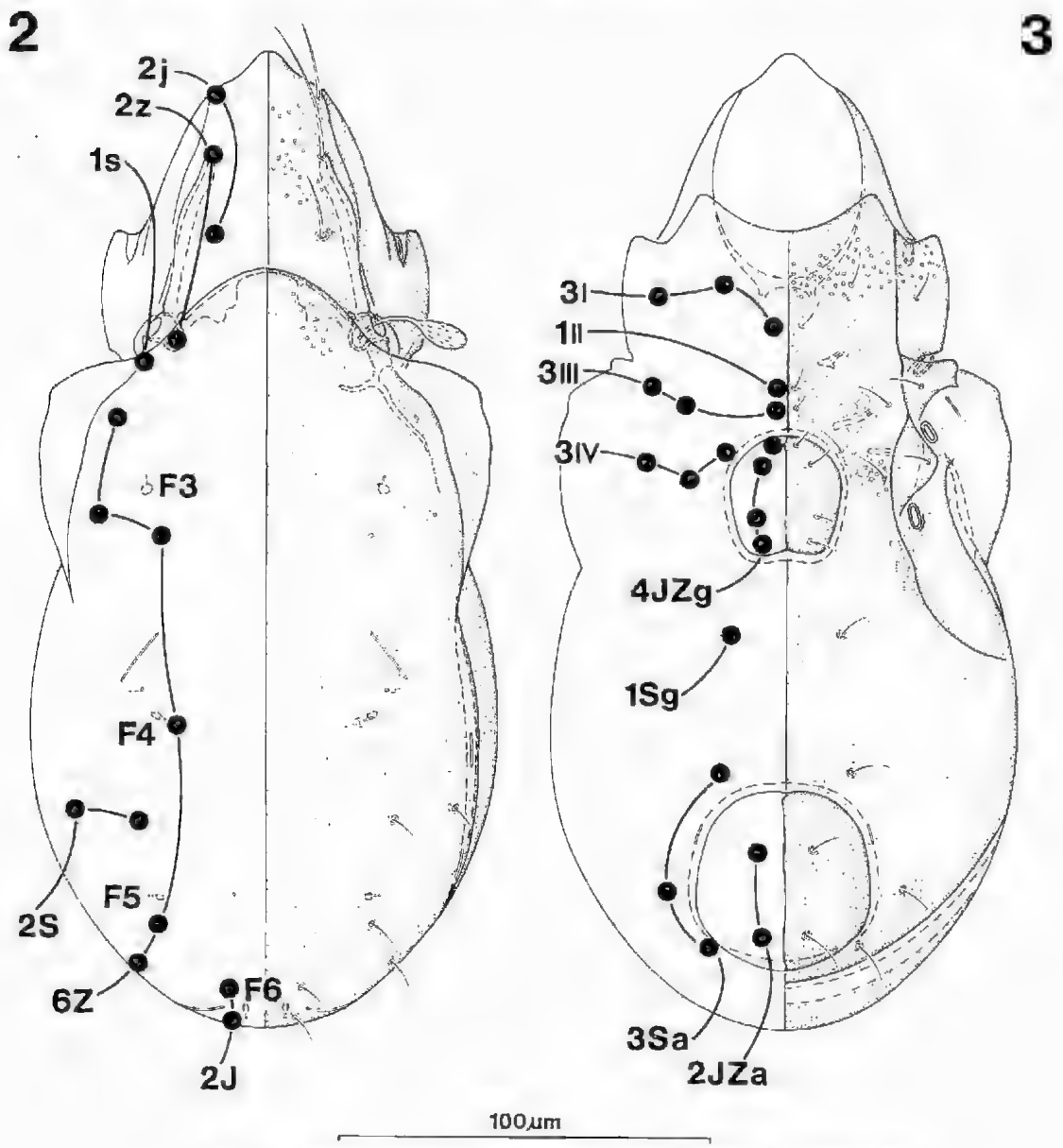
Incabates macronudus sp. nov.

Type material

Holotype female (SAMA N199121), plant litter, sparse moss and sandy soil, under sclerophyllous shrub amongst messmate stringybark (*Eucalyptus obliqua*), dry sclerophyll forest, near summit of Mt Lofty (34°59'S, 138°45'E), Cleland Conservation Park, 9.v.1974.

Female: Soma oblong, brown. Idiosomal length 446 (n = 1). Leg lengths (femur-tarsus for 446): I-178, II-163, III-142, IV-166. Tibial maximum heights (for 446): I-22, II-17, III-14, IV-14.

Proteronotum with narrow rostrum. Integument smooth. Sublamella obscured in dorsal aspect by laminar lamella. Tutorium absent. Sensory seta (z2)



Figs. 2, 3. *Incabates punctatus* sp. nov., female soma. 2, notum; 3, idiosternum

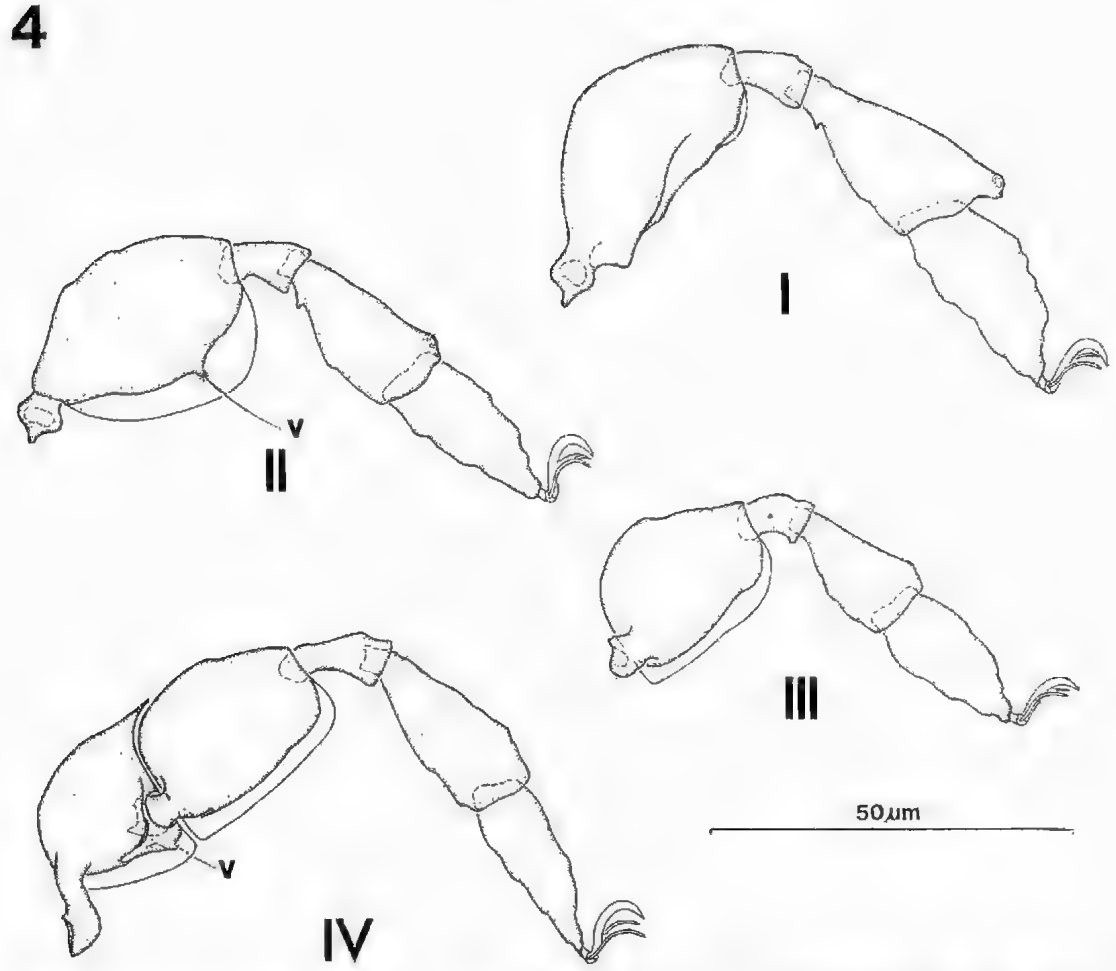


Fig. 4. *Incabates punctatus* sp. nov., female right legs I-IV, femur-pretarsus, also trochanter IV, posterior aspect. Only two setae illustrated (*v* = ventral).

clavate (caput may appear globular if viewed end on), caput subequal in length to exposed stalk. Subbothridial flange conspicuous. Posterior margin of bothridium raised to form tooth-like spur. Interlamellar seta (*j*2) longer than distance *j*2-*z*1. Hysteronotum with no obvious setae. Alveoli form clear refractile rings, microseta recognised in *Z*2, may be present elsewhere. Extra alveolus between *Z*2 and *Z*3 on right side only. Foramina with conspicuously refractile saccule, *F*3 oval and larger than other saccules.

Idiosternal setae fine and short, setae *I*3 and *Sa*1 the longest, setae III3 and IV3 not located. Integument smooth except for indistinct reticulations around ventrosejugal apodeme and apodeme III. Genital seta *JZg*2 midway between *JZg*1 and *JZg*3, rather than closer to *JZg*1. Discidium height less than 0.5× height of pedotectum II, coxite seta *IV*3 not located. Egg subellipsoidal, exochorion smooth, mean size 166 × 70 (n = 4), length 42% of somal length, four eggs in single female.

Legs short (median femur-tarsus length: 36% of somal length) with stout (mean maximum tibial height 39% of mean length). Trochanter IV with blunt process on angulate distodorsal margin which extends over femur IV.

Remarks: The name *macronudus* is from the Greek for 'large' and the Latin for 'naked' and refers to its body size and the absence of recognisable setae on the hysteronotum. *I. macronudus* is the only species known in *Incabates* with no easily observable hysteronotal seta (*I. nudus* has one pair) and with *I. major* it has a somal length greater than 440 µm. Because there is only one specimen, it was not dissected, which may explain why some coxite setae (*III*3 and *IV*3) have not been located.

Incabates punctatus sp. nov.

Type material

Types: Holotype female (SAMA N1987645), soil, plant litter and sparse moss under ridge-fruited mallee (*Eucalyptus incrassata*) clumps amongst broombush shrubs (*Melaleuca uncinata*), Ferries-McDonald Conservation Park (35°15'S, 139°09'E), 20.vi.1974. Paratypes, 45 females (SAMA N1987646 – N1987654, N199122 – N199142, five – BMNH, five – FMNH, five – NZAC) and 55 males (SAMA N1987655 – N1987671, N199143 – N199165, five – BMNH, five – FMNH, five – NZAC), as holotype.

Female: Soma oval, brown. Idiosomal length 259 (n = 25, Mallee broombush, 249-267), 257 (n = 2, Mallee heath, 256, 258) or 260 (n = 3, Sclerophyll forest, 252-267). Leg lengths (femur-tarsus, Mallee broombush, for 262): I-113, II-98, III-82, IV-105. Tibial maximum heights (for 262): I-16.5, II-13, II-11.5, IV-13.

Proteronotum with medium breadth rostrum. Integument punctate anterior to seta *j2*. Sublamella mainly obscured in dorsal aspect by laminar lamella. Costate tutorium present. Sensory seta (*z2*) clavate, caput subequal in length to exposed stalk. Subbothridial flange conspicuous. Posterior margin of bothridium raised to form small single or double tooth-like spur. Interlamellar seta (*j2*) shorter than distance *j2*-*z1*. Hysteronotum without obvious setae anteriorly (*Z1*, *Z2*, *Z3*, *Z4*) but microsetae recognised for *Z1* and *Z2*, whilst posterior small setae (*J5*, *J6*, *Z5*, *Z6*, *S5*, *S6*) present. Integument punctate anterior to pteromorphs. Foramina with conspicuously refractile saccule, *F3* spherical and larger than other saccules.

Idiosternal setae fine and short, variable relative lengths, but *1A*, *1B*, *JZg3* always shortest. Integument with indistinct reticulate sculpturing and punctate in coxisternal region. Genital seta *JZg2* closer to *JZg1* than *JZg3*. Discidium height more than 0.5× height of pedotectum II, coxite seta *4V3* level with, and close to apex. Egg subellipsoidal, exochorion smooth, mean size 132 × 64 (n = 13), length 49% of somal length, usually one egg per female (n = 14), two eggs in single female.

Legs short (median femur-tarsus length: 38% of somal length) with very stout girth (mean maximum tibial height 51% of mean length). Trochanter IV with sharp process on angulate distodorsal margin which extends over femur IV.

Male: Similar to female but idiosomal shorter, mean length, 239 (25, Mallee broombush, 226-252), 249 (5, Mallee heath, 238-250), 251 (3, Coastal, 250-253) or 247 (3, Sclerophyll forest, 244-252).

Referred material: Three females (SAMA N1987672, N199174, N199175) and five males (SAMA N199176 – N199180), sand, plant litter, under Banksia shrubs (*Banksia ornata*), amongst other sclerophyllous shrubs and sparse brown stringybark mallee (*Eucalyptus baxteri*), Tamboore Homestead (35°57'S, 140°29'E), nr Mt Rescue Conservation Park, 4.vii.1974.

Three males (SAMA N199171 – N199173), soil, plant litter and sparse grass under coastal wattle (*Acacia sophorae*), Piccaninnie Ponds Conservation Park (38°03'S, 140°57'E), 3.vii.1974.

Three females (SAMA N199166 – N199168), two males (SAMA N199169, N199170), plant litter, sparse moss and sandy soil, under sclerophyllous shrub amongst messmate stringybark (*Eucalyptus obliqua*), dry sclerophyll forest, near summit of Mt Lofty (34°59'S, 138°45'E), Cleland Conservation Park, 9.v.1974.

Remarks: The name *punctatus* is from the Latin for 'dotted' and refers to what may be small pits on anterior parts of the soma, which are more extensive than in other species. Also *I. punctatus* is unique within the genus in lacking four anterior pairs of hysteronotal setae (microsetae may be present), whilst the posterior six pairs have small setae, that are relatively long for *Incabates*. *I. pahabaeus* Corpus-Raros, 1980 is similar but without such a clear difference in size between the two groups of setae. Also, on *I. pahabaeus*, the interlamellar setae are much longer and the hysteronotal slit-shaped pore *hf3* is short and not as long as seta *J6*.

Genus *Setincabates* gen. nov.

Type-species: *Setincabates hypersetosus* sp. nov.

Definition: Haplozetidae. Hysteronotum with 13 pairs (*4J*, *6Z*, *3S*) of medium-sized setose setae. Hysteronotal foramina with saccule bag-like, gradually tapering to pore. Dorsosejugal furrow entire. Translamella, prelamella and tutorium absent. Rostral seta (*rl*) directly in front of lamellar seta (*zl*). Pteromorph movable, with clear weakly sclerotized basal line. Discidium triangulate. Tibia I with large solenidium (*so2*) on tubercle. Tibia II without distodorsal spur. Genu I and II with two setae (*v* absent). Trochanter IV with distodorsal process extended over femur IV, distodorsal crown with only anterior angulate lobe, broad flange extending along entire venter of caput. Pretarsus with three claws, slimmer lateral claws with pointed tip.

Distribution: Australia (Aa). Only record from South Australia, at site which amongst those sampled has the highest rainfall.

Remarks: The name *Setincabates* has the prefix *Set*, an abbreviation of the Latin seta for 'bristle or hair', and refers to the presence of more hysteronotal setae on the single included species than on members of the similar *Incabates* and other haplozetine genera with short or medium-sized setae. The haplozetine *Flagellobates* Mahunka, 1978 with long hysteronotal setae has 14 pairs of hysteronotal setae. Some other subfamilies included in Haplozetidae by Balogh & Balogh (1984) have similarly numerous hysteronotal

setae. Members of the Peloribatinae, all of which have long hysteronotal setae, have either 14 pairs or, in *Acutozetes* Balogh, 1970, 13 pairs of hysteronotal setae (possessing six not five setae in file *J*). The only other haplozetid species with more than 10 pairs of hysteronotal setae are members of the *Pilobates* Balogh, 1960 (Pilobatinae) with 14 pairs and six pairs of genital setae and a straight, transverse complete ventrosejugal apodeme and one species of *Rostrozetes* Sellnick, 1925 (Rostrozetinae) with 14 pairs and a short fissure-like pore *hf*3 similar in length to the hysteronotal foramina. The character states of *Setincabates* recognised here as distinguishing it from *Incabates* are probably primitive.

Setincabates hypersetosus sp. nov.

Type material

Types: Holotype female (SAMA N199181), plant litter, sparse moss and sandy soil, under sclerophyllous shrub amongst messmate stringybark (*Eucalyptus obliqua*), dry sclerophyll forest, near summit of Mt Lofty (34°59'S, 138°45'E), Cleland Conservation Park, 9.v.1974. Paratypes, 21 females (SAM N199182 – N199196, two – BMNH, two – FMNH, two – NZAC) and 21 males (SAM N199197 – N199111, two BMNH, two – FMNH, two – NZAC), as holotype.

Female: Soma oval, brown. Idiosomal length 264 (22, 254-275). Leg lengths (femur-tarsus for 267): I-122, II-104, III-86, IV-110. Tibial maximum heights (for 267): I-19, II-13, III-13, IV-14.

Proteronotum with broad rostrum. Integument smooth except for punctuations on gnathosternum between postoral setae. Sublamella mainly obscured in dorsal aspect by laminar lamella. Tutorium not present, although short ridge present around base of rostral setae (*j*1). Sensory seta (*z*2) clavate, with long ellipsoidal caput more than twice length of exposed stalk. Sub-bothridial flange conspicuous. Posterior margin of bothridium rounded without tooth-like spur. Interlamellar seta (*j*2) about ×2 distance *j*2-*z*1. Hysteronotum with 14 pairs of small setae (5*J*, 6*Z*, 3*S*). Foramina with small oval refractile saccule without parallel sided duct, all similar in size.

Idiosternal setae fine and short, peripheral setae longer, *I*2 and *JZa*3 longest. Integument with indistinct reticulate sculpturing in coxisternal region. Genital seta *JZg*2 closer to *JZg*1 than *JZg*3. Discidium height less than 0.5× height of pedotectum II, coxite seta *IV*3 near, but posterior to apex. Egg subellipsoidal, exochorion smooth, mean size 132 × 65 (n = 4), length 49% of somal length, one egg per female.

Legs short (median femur-tarsus length: 40% of somal length) with very short girth (mean maximum tibial height 54% of mean length). Trochanter IV with short sharp process on angulate distodorsal margin which just extends over femur IV.

Male: Similar to female but idiosoma shorter, mean length, 239 (21, 244-285).

Remarks: The name *hypersetosus* is the Latin for 'bristly' or 'setose' with the Greek prefix for 'beyond' or 'over' and refers to the unusually extensive hysteronotal setation compared with members of genera similar to *Setincabates*.

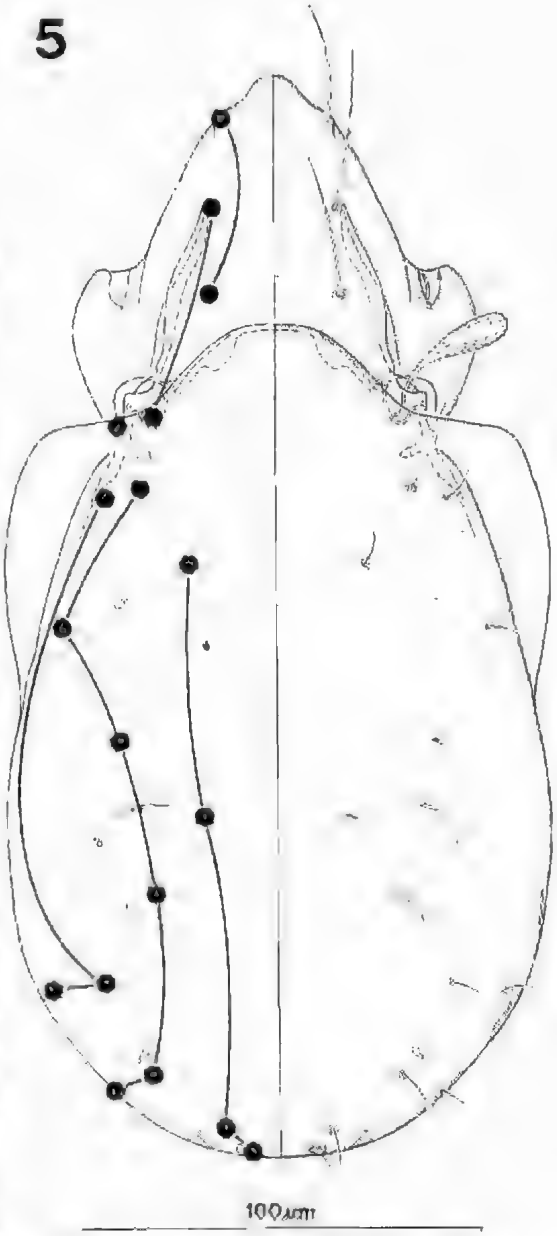


Fig. 5. *Setincabates hypersetosus* gen. & sp. nov., female soma, notum.

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BRYOZOA IN COORONG - TYPE LAGOONS, SOUTHERN AUSTRALIA

*BY MARGARET SPRIGG & YVONNE BONE**

Summary

Unilaminar, multiserial colonies of living Bryozoa *(Conopeum aciculata)* are widespread throughout the Coorong Lagoon, South Australia. The bryozoan is an opportunistic species that is able to tolerate variable salinities. It establishes itself early in spring and reaches maturity prior to the drying-out of its nearshore environment in late summer, whereupon it dies. It is intimately associated with serpulid growth in the northern Coorong Lagoon. *C. aciculata* has also been found growing in the hyposaline waters of Lake Clifton, Western Australia, where it is found within clotted, calcareous thrombolites. The age of the Lake Clifton bryozoan colonies is unknown.

Sub-Recent buildups of *C. aciculata* are extensive along the north-eastern side of the Coorong Lagoon, between Magrath Flat and 2.5 km south of Salt Creek. The colonies are multiserial and multilayered. The architecture of these buildups differs, with those in the northern lagoon being densely packed, flat to globose coalescing mounds whereas those in the more saline southern lagoon are loosely packed, highly contorted and convoluted "pavements". Serpulid association with these Sub-Recent bryozoans is minor.

KEY WORDS: Bryozoa, Coorong, hypersaline lakes, buildups, serpulids.

Transactions of the Royal Society of S. Aust. (1993), 117(2), 87-95.

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by MARGARET SPRIGG & YVONNE BONE*

Summary

SPRIGG, M. & BONE, Y. (1993) Bryozoa in Coorong-type lagoons, southern Australia. *Trans. R. Soc. S. Aust.* 117(2) 87-95, 4 June, 1993

Unilaminar, multiserial colonies of living Bryozoa *(Conopeum aciculata)* are widespread throughout the Coorong Lagoon, South Australia. The bryozoan is an opportunistic species that is able to tolerate variable salinities. It establishes itself early in spring and reaches maturity prior to the drying-out of its nearshore environment in late summer, whereupon it dies. It is intimately associated with serpulid growth in the northern Coorong Lagoon. *C. aciculata* has also been found growing in the hyposaline waters of Lake Clifton, Western Australia, where it is found within clotted, calcareous thrombolites. The age of the Lake Clifton bryozoan colonies is unknown.

Sub-Recent buildups of *C. aciculata* are extensive along the north-eastern side of the Coorong Lagoon, between Magrath Flat and 2.5 km south of Salt Creek. The colonies are multiserial and multilayered. The architecture of these buildups differs, with those in the northern lagoon being densely packed, flat to globose coalescing mounds whereas those in the more saline southern lagoon are loosely packed, highly contorted and convoluted "pavements". Serpulid association with these Sub-Recent bryozoans is minor.

KEY WORDS. Bryozoa, Coorong, hypersaline lakes, buildups, serpulids.

Introduction

The southern Australian continental shelf and its coastal inlets (Fig. 1a) have provided an ideal environment for prolific bryozoan growth and preservation throughout the Cainozoic Era. Accumulations of their calcareous skeletons attain great thicknesses over tens of thousands of square kilometres of both open water and protected embayments. Their deposits extend from high-tide levels about protected and open coasts to beyond the edge of the continental slope (James & Bone 1992; Bone & James 1993).

The extension of bryozoan growth into sub-coastal lagoons is less well known. Today, an encrusting cheilostome anascan, *Conopeum aciculata* (MacGillivray, 1891), is found in South Australia's Coorong Lagoon (Fig. 1b), where it tolerates salinities that range from well below sea-water through to hypersaline. This bryozoan was formerly reported as *Membranipora aciculata* (Bone & Wass 1990; Bone 1991), but has now been confirmed as *C. aciculata*. A millenium ago it thrived in the Coorong waters when they were only marginally more saline than the sea.

Another occurrence of what is believed to be the same species (Bock pers. comm.) has recently been discovered in hyposaline portions of Lake Clifton, about 100 km south of Perth, Western Australia (Fig. 1c). The sub-Recent history of the Lake Clifton example is not known.

Interestingly, both occurrences are found in sub-coastal interdunal lagoons facing open oceans in mid-30 degree south latitudes. Both lagoonal systems are subject to a degree of ground water drainage via highly porous and permeable, semi-consolidated, aeolianitic, Pleistocene back-shore beach dunes. Both lagoons are similar in that significant salinity differences are manifested along their length, and these fluctuate according to seasonal water influxes. Holocene dolomite is found in both systems (Rosen & Coshell 1992). Lake Clifton was probably once a continuation of the present day Harvey Estuary (Moore *et al.* 1984) into which River Murray waters from the adjacent Darling Ranges flow at its northern, Peel Inlet end, but it is now cut off from the sea.

The Coorong still receives influxes of water directly from both the sea and its own Murray River. Although the Coorong and Lake Clifton environments possess these basic similarities, they also have significant differences in detail and salinity fluctuations which affect bryozoan establishments and growth.

In this paper, the Bryozoa and their environments are compared and summarised, with the emphasis placed on the Coorong example.

Geological Settings

The Coorong linear lagoons and Lake Clifton are products of repeated oscillation of Quaternary sea level and regional tectonic uplift. This has resulted in a sequence of abandoned sea beaches across a width suitable to create significant separation of respective sea coasts and their fossilised backshore dune deposits, both on and off-shore. This is more apparent in the South Australian example.

The present Coorong Lagoon lies in the latest interdunal corridors of successive strandings of parallel ocean-beach and backshore dunes of the Bridgewater

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Formation. This is a highly calcareous cross-bedded medium to coarse grained aeolianite. (Sprigg 1952). Similarly, Lake Clifton lies between linear shore-parallel Pleistocene ridges of calcareous sandy Tamala Limestone. These ridges show large scale cross bedding, and are composed of fine to coarse grained skeletal-fragment calcarenite with variable amounts of quartz sand (Playford & Leech 1977).

In both the Coorong and Lake Clifton regions fossil soils with rhyzoliths have developed at various levels

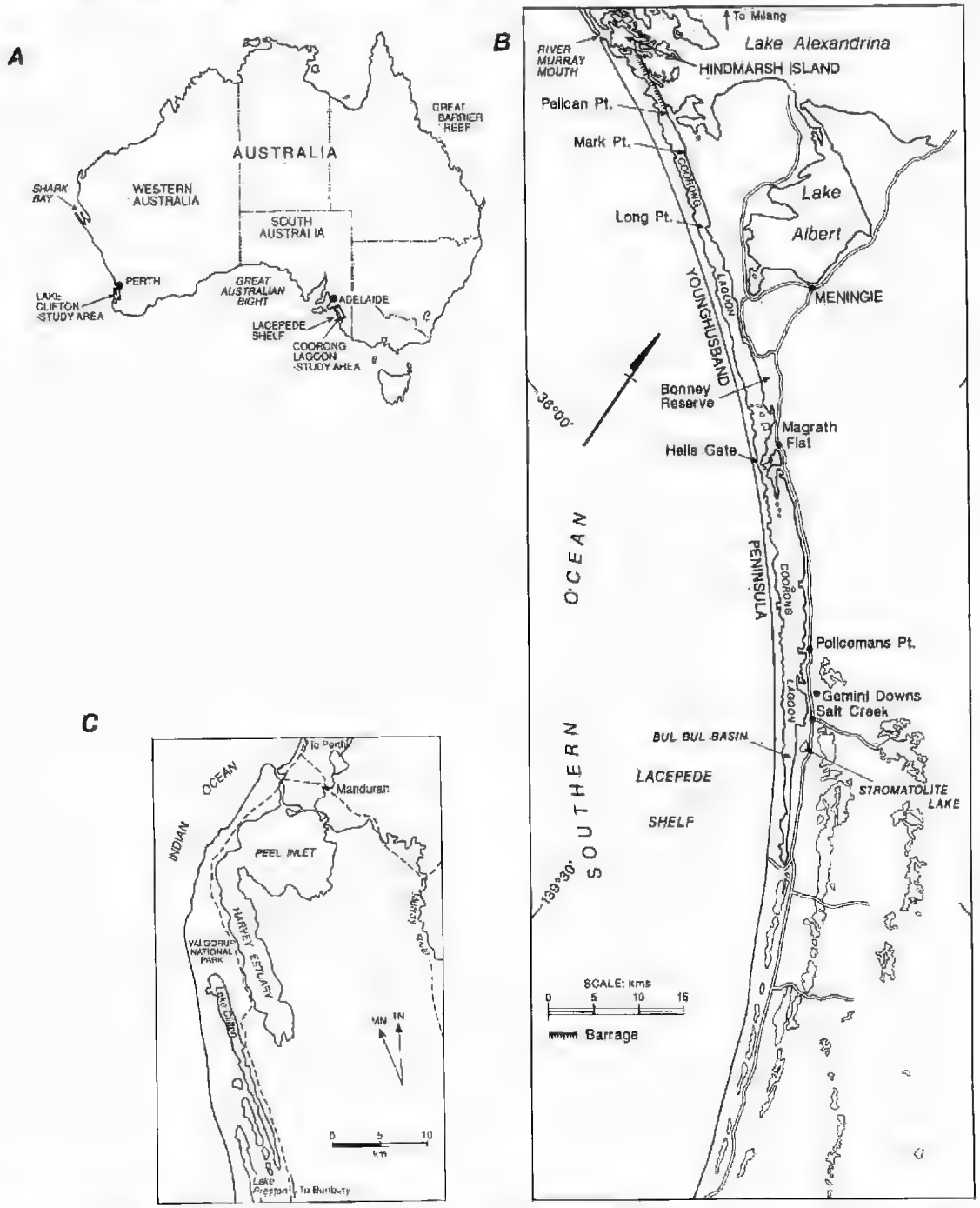

Fig. 1. Ia: Map of Australia showing the locations of the Coorong Lagoon and the Lake Clifton area. Ib: Coorong Lagoon Location Map. Ic: Lake Clifton Location Map.

within the dunes. These dunes in places include calcretised layers, if the soil forming periods were of sufficient duration. The Lake Clifton Tamala Limestone has calcrete-lined solution pipes (Semeniuk & Searle 1985) that are similar to those in the Coorong (Bone & Wass 1990). These solution pipes are features of calcrete profiles, and are formed tube-like, by calcium carbonate precipitation around regions of net vertical water percolation (Scholle *et al.* 1983) through limey dunes. In the Coorong area, erosion has removed much of the original dunes so that many of these large solution pipes are free standing by the water's edge, where they appear like the remains of petrified forests.

The Coorong and Lake Clifton interdunal areas were both inundated by the sea during the Holocene, and in each case, the consolidated aeolianites or their calcrete cappings provide excellent bases for biohermal buildups (Fig. 2).

The Lake Clifton example

The rise in sea level during the Holocene caused some of these shore-parallel limestone ridges in the southwest of Western Australia to become inundated and form a lakeland system of linear barrier estuaries and lagoons, including Lake Clifton (Fig. 1c; Searle & Semeniuk 1985). The ridges, which enclose the lagoon and separate it from the Indian Ocean 1.5 km away, dip below sea level just north of the lake and run across the narrow bryozoan-rich sediments of the Rottnest Shelf (Collins 1988) to re-emerge at Rottnest Island (Playford & Leech 1977).

The 21.5 km long, 1.0 km wide lake is replenished by winter rains falling directly on to it and by underground water from an extensive aquifer along its eastern shore. The lake is shallow, much of it being less than 1.0 m and a maximum of 3.0 m deep (Fig. 3). Water levels seasonally fluctuate up to a metre, periodically exposing and desiccating the large areas of thrombolites growing there.

A bryozoan, tentatively identified as *C. aciculata*, intimately grows over and through the clotted calcareous thrombolites (Fig. 4). The largest colony found was 2 cm in diameter. The thrombolites (Burne & Moore 1987) outwardly appear similar to stromatolites and are constructed in part by the trapping and binding of detrital sediment by cyanobacteria. As well as supporting Bryozoa, the lithoherms provide shelter for communities of fish, amphipods, isopods, decapods, nerid worms and various insects. The spaces between the clots often become filled with sediment rich in small gastropod (e.g. *Coxiella* sp.) and ostracod shells.

The salinity of Lake Clifton remains less than that of sea water throughout the year, though other lakes in the same system range from hyposaline to hypersaline. Their salinity and water chemistry, and that of the regional ground water, were investigated by Moore (1987) to elucidate why thrombolites were restricted to Lake Clifton. She found the waters of

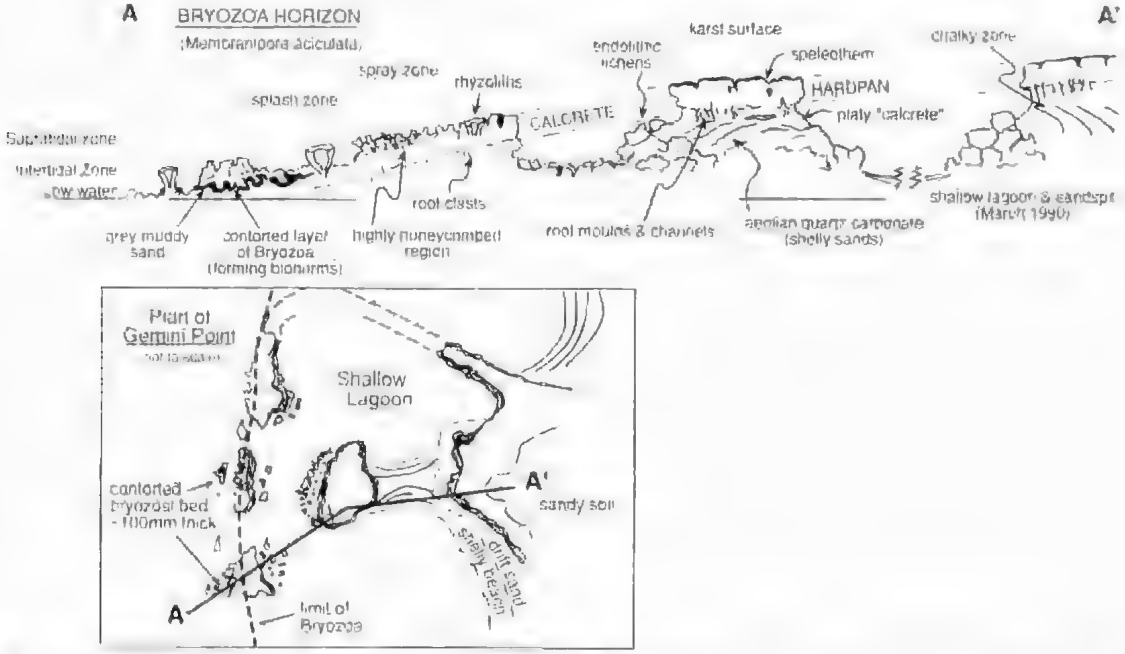

Fig. 2. Gemini Downs, Coorong Lagoon. Section A-A', through headland, showing relationship of bryozoan bioherms to calcretised aeolianites.

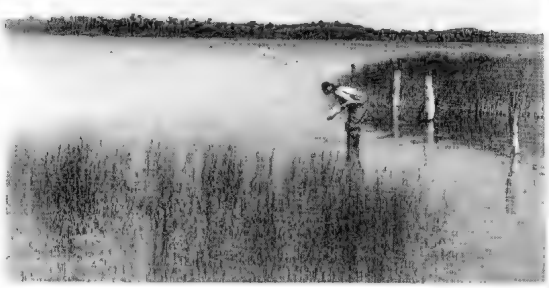

Fig. 3. Lake Clifton shallow water, hyposaline environment - reeds at margins in contrast to Chenopodiaciae rimming the Coorong Lagoon. Figure (holding a thrombolite) for scale.

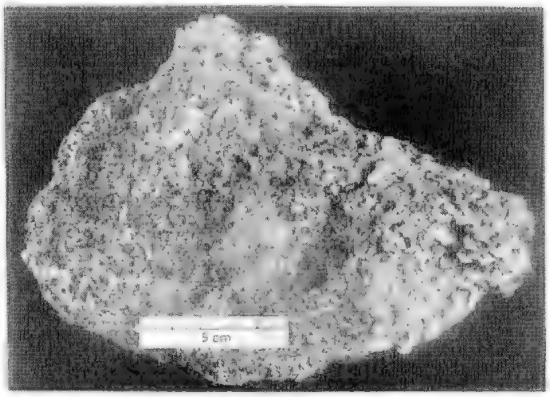

Fig. 4. Clotted, calcareous thrombolite from Lake Clifton. The bryozoan *Conopeum aciculata* is most densely intertwined in the central portion of the thrombolite.

all the lakes had ionic compositions proportionally similar to sea water, but that Lake Clifton, which receives virtually no surface run-off, obtains a large volume of its annual water from low salinity (1-2%) ground water. This water is enriched in calcium and bicarbonate (Moore 1984) which locally modifies the chemical composition of the sediment-water interface. Moore (1987) found the calcified thrombolites were consistently associated with the aquifer's discharge area along the lake's eastern shore. It follows that this, then, must also apply to the Bryozoa. Her study suggested the debouching ground waters provide a chemical environment conducive to the formation of the thrombolites that the Bryozoa encrust.

The Coorong example

Geological Setting

The Coorong (Fig. 1b) is a modern artefact of an ongoing process of successive strandings of ocean-beach backshore dunes straddled across the northern limb of the regionally uplifting Mt Gambier Arch. This uplift resulted in Tertiary seas withdrawing from the Murray Basin. Relatively rapid sealevel oscillation in response to dramatic climatic change left sub-parallel coastlines which can be tied to Milankovitch insolation signatures (Sprigg 1979; Idnurm & Cook 1980). These roughly coincide with the perturbation cycles in the earth's orbit during the late-Quaternary.

A sequence of "palaeo Coorongs" exists between ocean-beach backshore dunes to the east of the present Coorong system. These dunes have been preserved by uplift and low surface drainage over the Tertiary karst topography.

Sediment cores taken from the Coorong suggest that initially the Coorong was a protected-marine environment, becoming progressively more restricted and subject to harsh salinity fluctuations (Gostin *et al.* 1988). Stable ^{18}O isotope studies of the sub-Recent buildups of *C. aciculata* in the Magrath Flat area indicate that the Coorong was only marginally more saline than sea water when the Bryozoa grew there around a millennium ago (Bone & Wass 1990).

Later low stands of sealevel have resulted in the

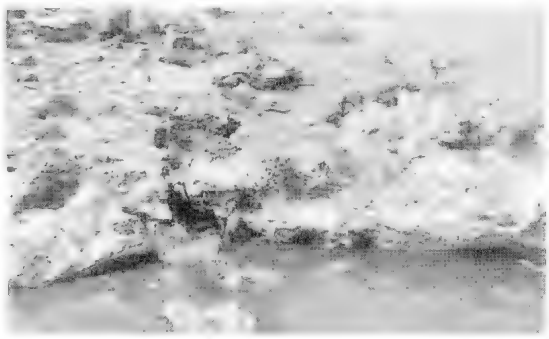

Fig. 5. Sub-Recent laterally extensive buildup of *Conopeum aciculata* in the Coorong Lagoon. Width of photo is 3 m.

Fig. 6. Colonies of *Conopeum aciculata* encrusting bottle found at Magrath Flat in early 1990.

exposure of earlier formed carbonate flats (von der Borch 1976). These form terraces around both major lagoons and also around the extensively eroded and modified beach that forms an intervening string of shoals and islands in the southern Lagoon. These latter lie between the Younghusband Peninsula barrier beach-dune system and the earlier consolidated backshore calcareous dunes.

Hydrology

The elongate nature of the Coorong estuary in an area of low, winter rainfall and high, summer evaporation, and the restriction of waterflow between its two major lagoons, results in a longitudinal salinity gradient, increasing southwards (Noye 1974). This is compounded by slow mixing of less dense river water from the Murray, flowing over denser Coorong waters when levels between the sea and lagoon are appropriate (Geddes 1987). Tide, wind direction, currents, irregular bottom topography and barrage openings all contribute to the south-eastern portion remaining hypersaline year round (Noye 1974).

Unlike Lake Clifton, however, groundwater seepage via aquifers to the Coorong, although probably significant, is minor compared to the high evaporation rate (Jensen *et al.* 1984; Noye 1974). Although drainage earlier this century around Salt Creek introduced some freshwater into the Coorong for a short period, water quality in the early 1980s was probably similar to pre-drainage (Jensen *et al.* 1984), from the time of early exploration of the area through until 1864. If so, it seems that for at least a century salinities affecting bryozoan growth have been similar to those of today, and that even weir and barrage construction (1920s and 1930s respectively) may not have radically altered conditions. Prior to this, in periods of drought when the Murray dried up, the Coorong would have become saline, and major floodwaters reaching the mouth would have freshened the lagoons, just as happens today.

Salinity peaks have been noted to gradually increase over a period of years (Jensen *et al.* 1984). Such increases are terminated by the release of large quantities of Murray waters during the spring of years of heavy flooding upstream. Some of these waters reach and freshen the southern reaches of the Coorong before the cycle begins again (Jensen *et al.* 1984).

Bryozoa

In 1987 Bone discovered laterally extensive sub-Recent multi-laminar buildups (Fig. 5) of encrusting anascan cheilostome Bryozoa. Individual buildups are up to 40 cm in diameter and 30 cm high. The most extensive bioherm growth visible centres on Magrath Flat (Fig. 1c). The bryozoan was identified as *Membranipora articulata* (MacGillivray 1891), but it is now suggested that it belongs to the genus *Conopeum*.

From mid-1987 to mid-1989 rare small scattered colonies (1 cm diameter) were found living intergrown with the serpulid, *Ficopomatus enigmaticus* (Fauvel), along the eastern margin of the Coorong from the Murray River to 2 km north of Policemans Point. The range of the living serpulids, however, was found to extend to Salt Creek (Bone & Wass 1990). In Spring 1989, conditions were apparently more advantageous for the bryozoan. It was found at Magrath Flat thriving on almost every hard surface, from the consolidated aeolianite of relict sand dunes, to bottles (Fig. 6) and tyres. Colonies up to 6 cm in diameter were found, but only as unilaminar forms (Bone 1991). Later the same year, serpulids out-competed the Bryozoa to completely cover and conceal all trace of sub-Recent bryozoan buildups in this locality. The same occurred in 1991 with serpulid banks building on those of the previous year (Fig. 7). Thus, locating the sub-fossil bryozoan buildups in this area can be difficult even when their position is known because of the thick covering of serpulids. Searches during 1990-91 for new locations of the sub-Recent bioherms in the northern Lagoon proved fruitless because of the extent and thickness of these serpulid "banks". In 1991 in particular, for more than 20 km each side of Long Point, serpulids were prevalent in the shallows (Fig. 8). They were found in cauliflower-shaped groups of worm tubes attached to almost any point of hard substrate piercing the carbonate-rich muddy sands. They were even found colonising the handle attachment hole of an old pick, growing out from it in opposite directions (Fig. 9).

Modern serpulid mounds range to >1.0 m in diameter, with multi-seasonal growth making some up to 0.5 m high. They form bioherms (Figs 7 & 8) with many other animals additional to the Bryozoa, such as crabs, isopods, copepods, amphipods, decapods, nerijd worms (e.g. *Ceratonereis aequisetis* Augener, 1913) and occasionally relatively large fish.

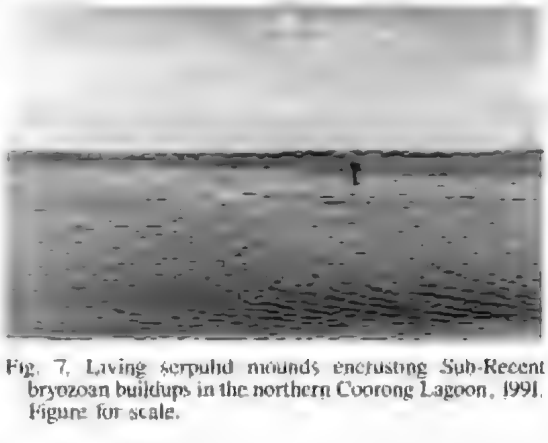

Fig. 7. Living serpulid mounds encrusting Sub-Recent bryozoan buildups in the northern Coorong Lagoon, 1991. Figure for scale.

Methods

Mapping of the areal extent of sub-Recent buildups of the bryozoan, *C. aciculata* in the Coorong was undertaken in concert with observation of its present day range. The eastern side of the Coorong Lagoon was mapped in detail, from Pelican Point to 8 km south of Salt Creek (Fig. 1b). A boat was used on several occasions to continue mapping around reefs and islands in the central part of the lagoon, and along the western shore.

Salinity measurements and observations of colony growth were made on a monthly schedule over two years, from points along the eastern coastline. Water samples were collected for analyses at the same time. These were analysed for their concentrations of sodium, potassium, magnesium and calcium by the atomic absorption method. The salinity of the same samples were tested by a Kent electrolytic conductivity meter, temperature corrected to 25°C, and converted to ‰ (total dissolved salts). Samples of very high salinity were diluted and the salinities re-scaled, as the meter used was poorly scaled at very high values.

Results

The water salinity analyses confirm the trends of earlier studies (Noye 1974; Geddes 1984, 1987; Botting 1990). Data is biased, as sample sites had to be along the eastern shoreline. Analyses of Na, K, Mg, and Ca showed the elements were roughly in proportion to seawater, but that usually Ca < K. A water sample from the River Murray (S.A.) had Ca > K.

Flooding of the Coorong by water released through the barrages stirred up the fine carbonate mud on the floor of the Lagoon, reducing visibilty to almost zero. This, plus the greater water depth, hampered the mapping aspect of the study. Location of the Bryozoa was often by touch and not by sight, so only a small number were found. However, these were sufficient to indicate that the buildups are widespread in the southern Lagoon.

Sub-fossil buildups were found at three separate levels. The highest and most altered level lies just below the high water mark, rimming the terraces previously mentioned. The middle level is generally found 20-30 cm lower. These become exposed in summer, lying about 15 cm above the lowest water level noted. The lowest level is found approximately 50 cm lower down.

In the northern Lagoon the sub-Recent *C. aciculata* buildups form densely packed semi-flat layers (Fig. 10). The buildups in the southern Lagoon have layers which are convolute, which result in spaces occurring between the more laminar layers (Fig. 11). These spaces often contain *Coxiella confusa* and other small gastropods, minute bivalves and many different ostracods, as well as foraminifera. The latter include *Ammonia beccarii*, *Elphidium articulatum* and *Discorbis dimidiatus*, which are marine fauna, and so may be indicative of much less saline water being present in this part of the Coorong at the time of bryozoan growth. Alternatively, they may have been re-worked from sub-Recent sand dunes (Cann pers. comm.). Oogonia, the fruiting bodies of non-marine charophytes (e.g. *Ruppia sp.*, which is tolerant to a wide range of salinities from fresh to hypersaline in the Coorong today – Womersley 1984) are also found within these spaces.

In both 1989 and 1990 the bryozoan Cyphonaute larvae had settled and begun to bud asexually by the beginning of October. In 1990 at the end of the first week in October colonies 1.0 cm in diameter were common and widespread, growing in the central southern Coorong, both along the shore and around islands, and on "reefs". The most southerly discovery of living *C. aciculata* was on the edge of the shallow hypersaline Bul Bul Basin, 4.5 km south of Salt Creek. These rare colonies were small encrustations on the sides of consolidated terraces belonging to earlier carbonate flats of a higher water level (Table 1).

Colony establishment time is not known for either year at the northern end of the study area at Pelican Point. At the northern end of the Coorong, small colonies (Table 1) were common both years in the fresh waters adjacent to the barrages, where lake waters are known to seep through.

A sketch and cross-section over the Point adjacent to the Gemini Downs Boat Ramp illustrate a typical southern Lagoon environment showing relationships between features and the sub-fossil accumulations (Fig. 2). These deposits are extensively intergrown around solution pipes, and some contorted bands (5-10 cm thick) contain teepee-like structures and possible fractures. They are underlain by grey, semi-plastic mud.

TABLE 1. *Size of colonies of modern* Conopeum aciculata *on north-eastern margin of Coorong Lagoon. Size differences were transitional between adjacent locations. "Warnecke Point" is an unnamed feature lying south of Hells Gate, on the Warnecke property.*

Location	Bryozoan Colonies — Maximum Size (cm)	
	1989	1990
Pelican Point	2.0	1.0
Mark Point	2.0	1.5
Long Point	–	1.5
Bonney Reserve	–	4.0
Magrath Flat	6.0	4.0
"Warnecke Point"	7.75	
Policemans Point Boat Ramp	3.0	3.0
Gemini Downs Boat Ramp	2.0 (rare)	2.75 (rare)
4.5 km south of Salt Creek	1.0 (rare)	1.5 (rare)

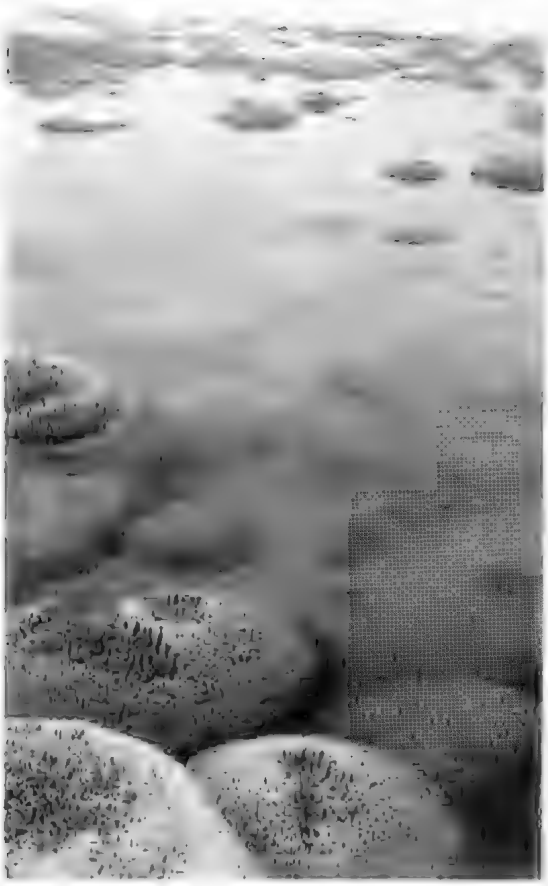

Fig. 8. Close-up of living serpulid mounds, showing their similarity to stromatolite growth form. The destruction of the upper, central portion is caused by fishermen dragging their boats across the bioherms. Individual mounds average 1 m in width

turn sharply and grow back on themselves, thus leaving "holes". Others were regularly laminated similar to those found in the northern Lagoon where one layer is laid down directly on the last. The growth of bryozoan colonies is largely affected by changes in their environment and this can cause changes in colony morphology (McKinney & Jackson 1989). Thus it may be possible to trace particular periods of environmental change over large areas of the lagoons through examination of the growth patterns of different buildups, if the contorted layers do indeed have a similar pattern at a particular time.

The three separate levels of buildups found in the southern Lagoon may have grown concurrently, but it is more likely that as water levels are known to have changed in the lagoons that each might belong to a different time period. High water levels prevented clear mapping of these different levels. Radiocarbon dating analyses currently being undertaken may elucidate these and other timing uncertainties.

Microfossils found within the convoluted layers of bryozoan buildups include Oogonia from algae characteristic of marginal marine and non-marine saline lakes. The Foraminifera are all extant, benthic species. Cann (pers. comm.) suggested (i) that they could have become encased by bryozoan growth after being washed in after eroding out of the surrounding aeolianite, or (ii) that having crawled there, the Foraminifera were trapped and died, as the fast growing *C. aciculata* entombed them.

New colonies found a week into October 1990 were common and widespread in the southern Lagoon. They were all about 1.0 cm in diameter. Colonies 0.2 cm larger or smaller than this were not present. Thus, a switching signal for the beginning of asexual budding must have occurred almost concurrently over a large area. Actual growth rate was not determined, as a precise settlement timing is not known, but growth certainly appears to have been rapid compared to that

Discussion

Due to conditions prevailing in the northern Lagoon favouring prolific growth of thick serpulid colonies in 1989 and 1990, searches of this area did not reveal new locations of sub-fossil Bryozoa. In the southern Lagoon, however, conditions were less beneficial to both serpulids and Bryozoa. In 1990 serpulid growth was less abundant than in the northern Lagoon, but 1991 brought even poorer growth. Consequently ubiquitious sub-fossil sub-Recent bryozoan buildups were often exposed in the southern Lagoon.

The convoluted nature of many of the layers of the sub-fossil bryozoan buildups found in the southern Lagoon were unusual in that instead of being parallel to each other like those found in the north, they were often highly contorted. Some twist upwards, only to

Fig. 9. Serpulid colony growing through the handle-hole of a pick-axe, found in the northern Coorong Lagoon in 1991.

Fig. 10. Common growth form of sub-Recent *Conopeum aciculata* in the northern Coorong Lagoon. The multilayered habit has flat layers densely packed and relief is low.

of most Bryozoa (McKinney & Jackson 1989). Growth ceases and the colony dies once it is exposed.

The rate of multilaminar layer formation is also unknown. Only one example of multilaminar growth was found in present day colonies. The colony is located on the internal walls of a solution pipe, where it is well protected from high energy wave and storm damage. It may be that multilayer growth occurred in the one season, or that growth of the second layer occurred in a later season coincidentally on the earlier skeletal remains.

Today, the living Bryozoa are only found growing on solid objects whereas many of the sub-fossil buildups form pavements (5-8 cm thick) that appear to have grown out laterally from the terraces, over the soft carbonate muds. Other bands, up to 20 cm thick, appear to have grown out laterally from consolidated aeolianite, so that now they are completely unsupported, other than for the hard rock they rim. It appears they may have originally grown over unconsolidated sediment, since eroded away.

Observations, coupled with analyses, show that very high salinities are lethal to *C. aciculata* . These high salinities occur early in summer in the southern Lagoon, resulting in maximum colony size being relatively small, especially compared to those in the northern Lagoon. This can be seen from Gemini Downs southwards to Salt Creek, where colony size ranges from 2.75 cm down to 1.5 cm, suggesting a very short growth period, particularly in 1990. The switch to the salinity level lethal to the organism could not be pinpointed, as samples were collected nearshore and thus did not always allow for local and daily salinity variations, due to slow mixing. However, even here daily variations are observed, confirmed by Botting & Associates (1990).

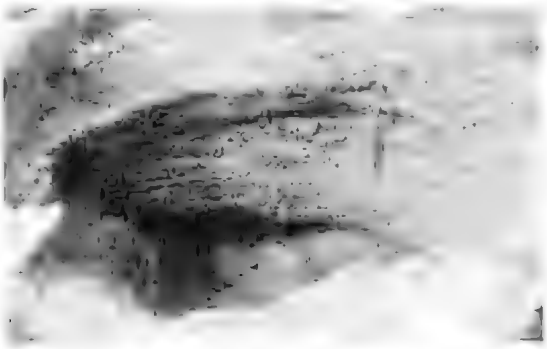

Fig. 11. Common growth form of sub-Recent *Conopeum aciculata* in the southern Coorong Lagoon. The multilayered habit is convoluted and distorted, and results in many buildups becoming fragmented.

Conclusions

1. Sub-Recent buildups of the bryozoan *Conopeum aciculata* are widespread in both the northern and southern lagoons of the Coorong. The buildups are up to 30 cm high and 40 cm in diameter. Growth form in the northern Lagoon is multiserial, multilayered, gently arcuate and compact. Growth form in the southern Lagoon is multiserial and multilayered but the layers are highly convoluted.

2. Modern colonisation of hard substrates in the Coorong by *C. aciculata* is seasonal, occurring in the spring; and even more widespread than the sub-Recent occurrences. Colony size increases rapidly, utilising multiserial, unilaminar growth form. Maximum colony size is 6 cm in diameter, occurring in the northern Lagoon. Serpulids frequently outcompete the Bryozoa, thereby concealing evidence of annual bryozoan presence.

3. Salinity in the Coorong increases southwards and increases seasonally up to 60‰, due to high evaporation in summer. The higher salinities are lethal to the Bryozoa but not to the serpulids. Similarly, exposure due to summer water-level fall kills the Bryozoan but not the serpulid colonies. Cyphonaute larvae are able to survive the high salinities, and re-colonise when conditions are optimal. Small bryozoan colonies occur in Coorong hyposaline waters adjacent to the fresh-water lakes at the northern reaches of the Coorong.

4. Modern *C. aciculata* occurs intimately associated with thrombolites in fresh water on the eastern margin of Lake Clifton, Western Australia.

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FEMALES AND IMMATURES OF THE AUSTRALIAN CADDISFLY HYALOPSYCHE *DISJUNCTA* NEBOISS (TRICHOPTERA), AND A NEW FAMILY PLACEMENT

BY A. WELLS & D. CARTWRIGHT†*

Summary

The female, larva and pupa of the northeastern Australian *Hyalopsyche disjuncta* Neboiss, 1980, are figured and described for the first time. Comparisons between *Hyalopsyche disjuncta* and several North American species of *Phylocentropus* Banks, 1907 (Family Dipseudopsidae Ulmer, 1904), show that both genera share apomorphous larval features. Transferral of *Hyalopsyche* Ulmer, 1904, from the family Hyalopsychidae Lestage, 1925, to the family Dipseudopsidae and supression of Hyalopsychidae are proposed.

KEY WORDS: Trichoptera, Dipseudopsidae, *Hyalopsyche*, larvae, pupae, females.

Transactions of the Royal Society of S. Aust. (1993), 117(2), 97-104.

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Summary

WELLS, A. & CARTWRIGHT, D. (1993) Females and immatures of the Australian caddisfly *Hyalopsyche disjuncta* Neboiss (Trichoptera), and a new family placement. *Trans. R. Soc. S. Aust.* 117(2), 97-104, 4 June, 1993.

The female, larva and pupa of the northeastern Australian *Hyalopsyche disjuncta* Neboiss, 1980, are figured and described for the first time. Comparisons between *Hyalopsyche disjuncta* and several North American species of *Phylocentropus* Banks, 1907 (Family Dipseudopsidae Ulmer, 1904), show that both genera share apomorphous larval features. Transferral of *Hyalopsyche* Ulmer, 1904, from the family Hyalopsychidae Lestage, 1925, to the family Dipseudopsidae and supression of Hyalopsychidae are proposed.

KEY WORDS: Trichoptera, Dipseudopsidae, *Hyalopsyche*, larvae, pupae, females.

Introduction

The history of unstable taxonomy of the group of polycentropodid-like caddisfly genera including *Dipseudopsis* Walker, 1852, *Protodipseudopsis* Ulmer, 1904, *Phylocentropus* Banks, 1907, and *Hyalopsyche* Ulmer, 1904, is discussed in detail by Weaver & Malicky (in ms). These authors present strong support for the familial status of Dipseudopsidae, including the first three of the above-mentioned genera, and possibly also *Hyalopsyche*, an African-Oriental genus, which was placed by Schmid (1980) with *Phylocentropus* in the family Hyalopsychidae. Convincing evidence for the monophyly of Dipseudopsidae Ulmer, 1904, *sensu* Weaver & Malicky, derives from a consideration of features of the female abdomens and larvae.

Although reference has been made in the past to females of *Hyalopsyche* (Ulmer (1915) identified three New Guinean female specimens as *H. rivalis* (Betten, 1909)), no descriptions of females are available, and until now no larvae have been associated.

A single Australian species of *Hyalopsyche*, *H. disjuncta* Neboiss, was described by Neboiss (1980) from two adult males from northern Queensland. Repeated efforts to collect more specimens, including larvae, failed; *H. disjuncta* appeared to be rare. Recently, however, during an intensive collecting trip of two week's duration in the Jardine River area of far northern Cape York (as part of the Royal Geographic Society of Queensland's "Wet Season" Cape York Peninsula Scientific Expedition), the authors collected numerous adults of both sexes, and just prior to departure, made the exciting find of several larvae and pupae. Female and larval and pupal features of this species are here described and illustrated, and the larval niche is described. For comparisons, some larval features of *Phylocentropus* sp., and the female genitalia and head showing the tentorium of the North American *P. lucidus* (Hagen) are also figured.

Confirmation of sharing of the specialised larval niche and other synapomorphous larval character states, firmly supports the monophyly of *Phylocentropus* — *Hyalopsyche*, and we present an hypothesis for the derivation of the specialised female genitalia of *Hyalopsyche* from those of *Phylocentropus*. We argue that *Hyalopsyche* should be placed in the family Dipseudopsidae *sensu* Weaver & Malicky (in ms), and the name Hyalopsychidae is here supressed.

Ross (1965) and Ross & Gibbs (1973) discussed the phylogenetic relationships of Dipseudopsinae (in the Psychomyiidae and subsequently in the Polycentropodidae), but with more data available, phylogenetic analyses of higher taxa of Trichoptera now in progress (Weaver & Frazer pers. comm.) should provide a more definitive assessment of the relationships of this family.

Materials and Methods

Adult *Hyalopsyche disjuncta* were taken mainly at 12v or 8v black or UV lights; adults and larvae were collected into and stored in 70% ethanol. Comparative material of the North American *Phylocentropus lucidus* (adults) was provided by Dr J.S. Weaver, and adults of *P. placidus* and *Dipseudopsis indicus* and larvae of *Phylocentropus* sp. were provided on loan by Dr J. Morse.

Specimens were prepared for study by treatment in caustic potash, or using a lacto-phenol preparation. Drawings were made using camera lucidas on a Wild

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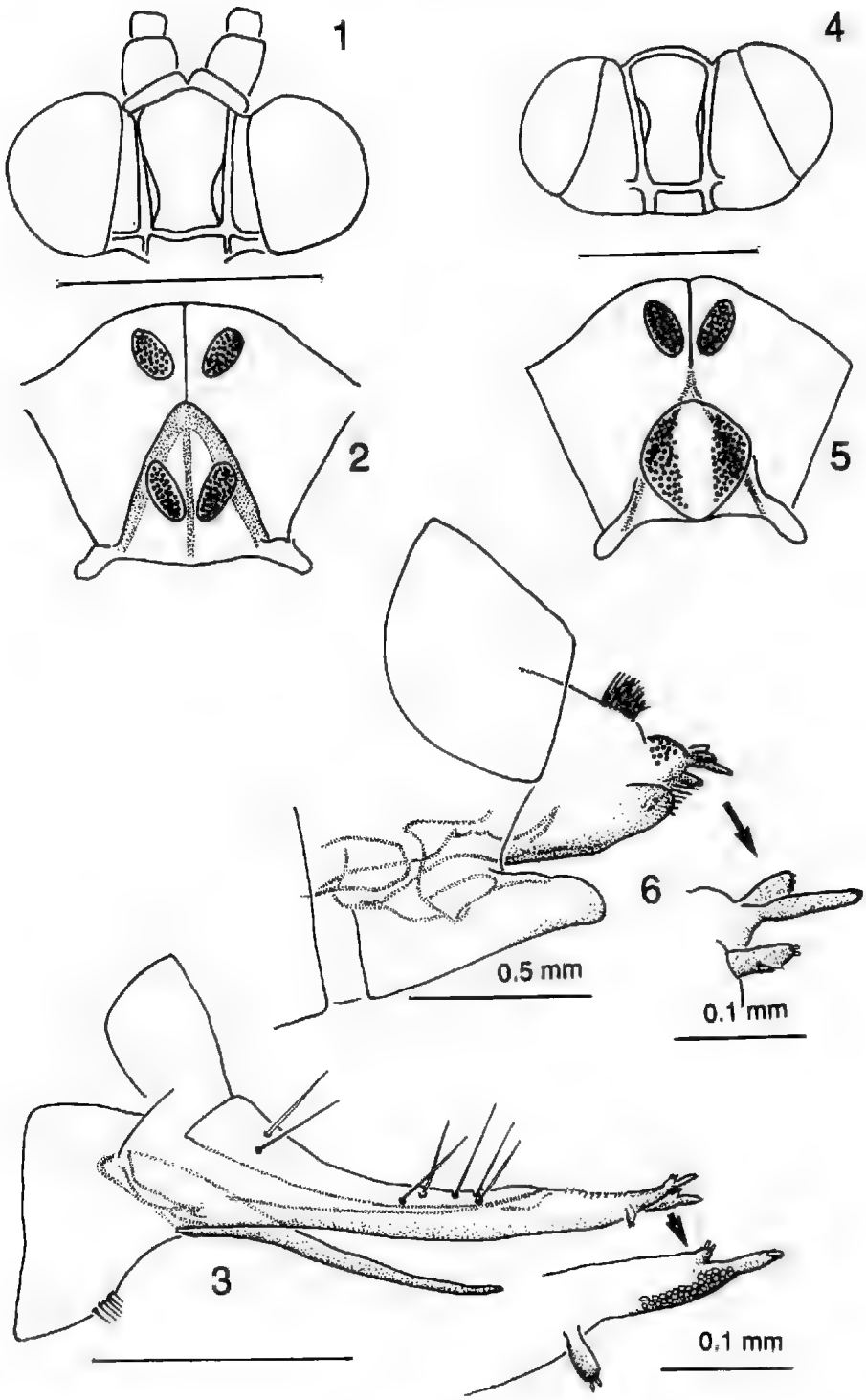


Figs 1-3. *Hyalopsyche disjuncta* Neboiss, female: 1, dorsal head showing tentorium; 2, mesothorax, dorsal view; 3, genitalia, lateral view.
Figs 4-6. *Phylocentropus lucidus* (Hagen), female: 4, dorsal head showing tentorium; 5, mesothorax, dorsal view; 6, genitalia, lateral view.
Scale bars = 1 mm, unless otherwise indicated.

M5 dissecting microscope and a Wild M20 compound microscope.

Material is deposited in the following institutions: Australian National Insect Collection, Canberra (ANIC); Museum of Victoria, Melbourne, (NMV); Northern Territory Museum of Arts and Sciences, Darwin, (NTM); and Queensland Museum, Brisbane, (QM).

Systematics

Hyalopsyche disjuncta Neboiss, 1980
FIGS 1-3, 7-13, 16, 18-21

Hyalopsyche disjuncta Neboiss, 1980: 357-361; Figs 1-8. Holotype male, N. Queensland, 29.iv.1979, NMV.

Material examined: N. Queensland: 1 ♂, 11° 50′S 142° 30′E, Bertie Creek, at Telegraph Crossing, 5.ii.1992, D. Cartwright and A. Wells, NTM; 2 ♂♂, 2 ♀♀, 11° 50′S 142° 30′E, Dulhunty River, at Telegraph Crossing, 8-9.ii.1992, D. Cartwright and A. Wells, NMV; 2 ♂♂, 1 ♀, 11° 39′S 142° 28′E, McDonnell-Cockatoo Creek jn, 18.ii.1992, D. Cartwright and A. Wells, NTM; 13 ♂♂, 5 ♀♀, 11° 44′S 142° 29′E, Gunshot Creek, at Telegraph Crossing, 17.ii.1992, D. Cartwright and A. Wells, QM; 11 ♂♂, 8 ♀♀, same loc. and collectors, 14-15.ii.1992, QM; 5 ♂♂, 15 ♀♀, same loc. and collectors, 18-19.ii.1992, NMV; 21 ♂♂, 4 ♀♀, same loc., 4-5.iv.1992, M. Crossland, ANIC; 31 ♂♂, 19 ♀♀, same loc. and collector, 10-11.iv.1992, NMV; 1 pupa, same loc., D. Cartwright and A. Wells, 18.ii.1992, NTM; 2 larvae, same loc. and collectors, NTM; 7 larvae (1 reared to adult ♀), 1 pupa, same loc. and collectors, 19.ii.1992.

Neboiss (1980) illustrates the general body features of male *Hyalopsyche disjuncta*, and gives anterior wing length as 6 mm, but in our samples male anterior wing length ranges from 4.3-6.2 mm. Females conform with males in general features, including reduced maxillary palpi and warts on the mesothorax (Fig. 2), but are considerably larger. An additional feature, the tentorium, is figured (Fig. 1); its arms are well developed, with inner lateral flanges posteriorly, and the posterior bridge complete.

Female (Figs 1-3). Anterior wing length 6.0-8.0 mm. Genitalia in the form of a slender, elongate, non-retractile ovipositor (Fig. 3). Sternite VIII not subdivided, external gonopod of segment VIII slender, tapered, reaching almost to tip of segment IX. Posteriorly segment X is divided to form a pair of distal lobes, each with apical cercus and one papilla partially fused on inner margin, the second projecting ventrally from the outer margin at about the level of division of segment X.

Larva (mature) (Figs 7, 8, 12, 13, 16, 18-20). Campodeiform, slender, elongate, (Fig. 7). Head, pronotum, limbs and anal claws brown-yellow or pale brown, dorsal margin of prothorax and strengthening ridges of thoracic pleura black, rest of body pale. Body length 6.0-14.8 mm, head capsule width 0.60-0.88 mm. Head round in dorsal view (Fig. 12); fronto-clypeus sub-triangular, extending to posterior of head capsule, anterior margin rounded, tentorial pits situated posteriorly; labrum broadly rounded with few setae, anterior margin finely divided. Mandibles (Fig. 16) stout, dissimilar, each with differing numbers of denticles apically and on inner distal margin, and with a dense penicillus medially on inner margin, antero-lateral margins crenulate; right mandible rugose antero-dorsally. On ventral head (Fig. 13), anterior ventral apotome (gula) short, forming an isosceles triangle; submentum rounded anteriorly, paired setae situated subapically; maxillary palps relatively slender, lobus internus broad, obliquely truncate in dorsal view, and bearing a brush of hair apically; labium modified to form a slender, elongate spinneret, about ⅔ as long as head capsule, labial palpi absent.

Prothorax only with sclerotised tergite. Fore trochantin fused to pleuron (Fig. 18). Mesosternum (Fig. 8) with a pair of elongate sclerites posteriorly.

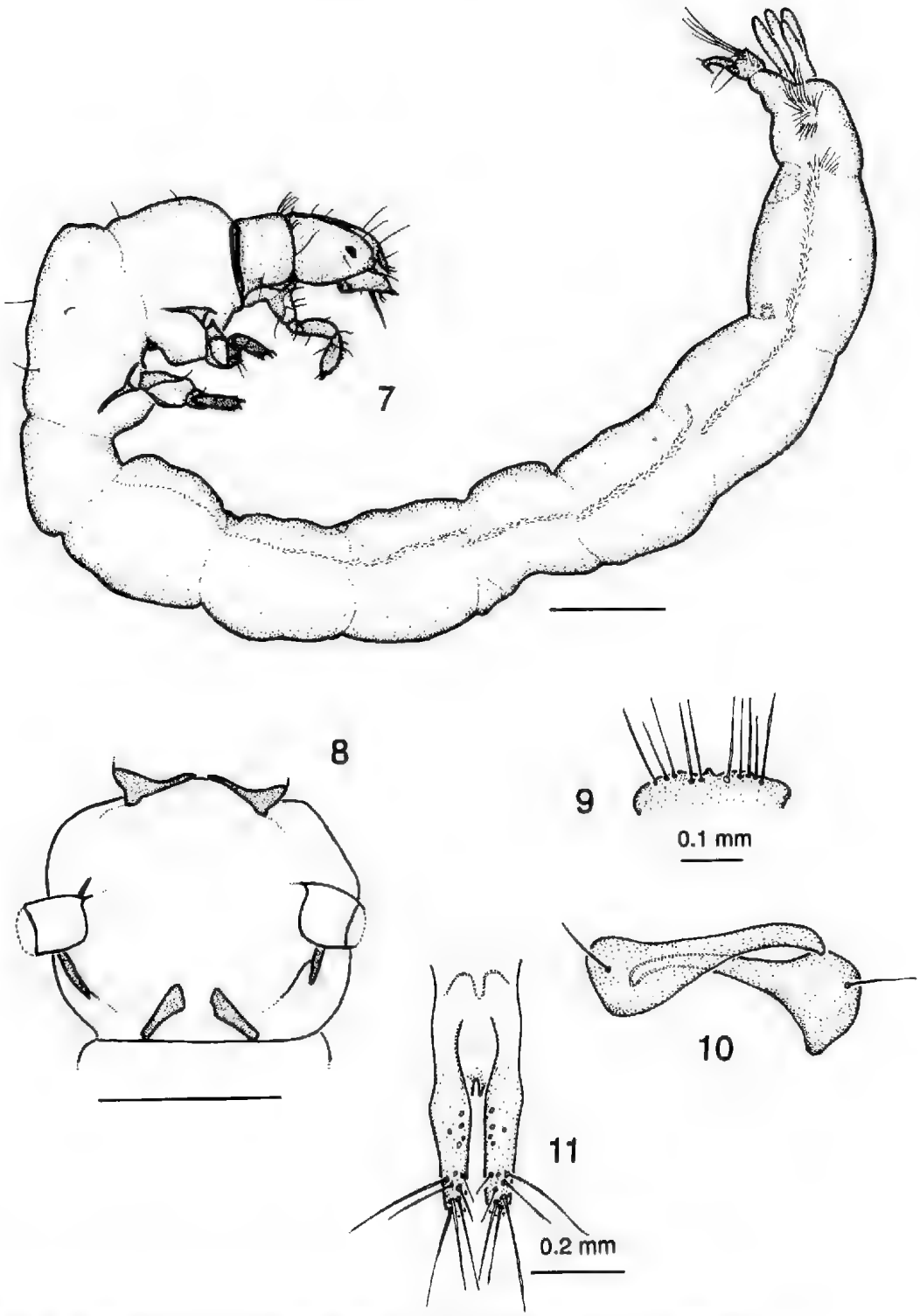
Legs (Figs 18, 19) short, flattened, tarsi with dense fringes of setae, claw on fore limb strongly curved. Fore tarsus with an adpressed row of modified setae on the mesial margin.

Abdomen elongate, with a lateral fringe of fine setae, without gills, but with a group of anal papillae (Fig. 7); anal prolegs elongate, with cluster of long setae anterior to the slender strongly curved anal claw (Fig. 20).

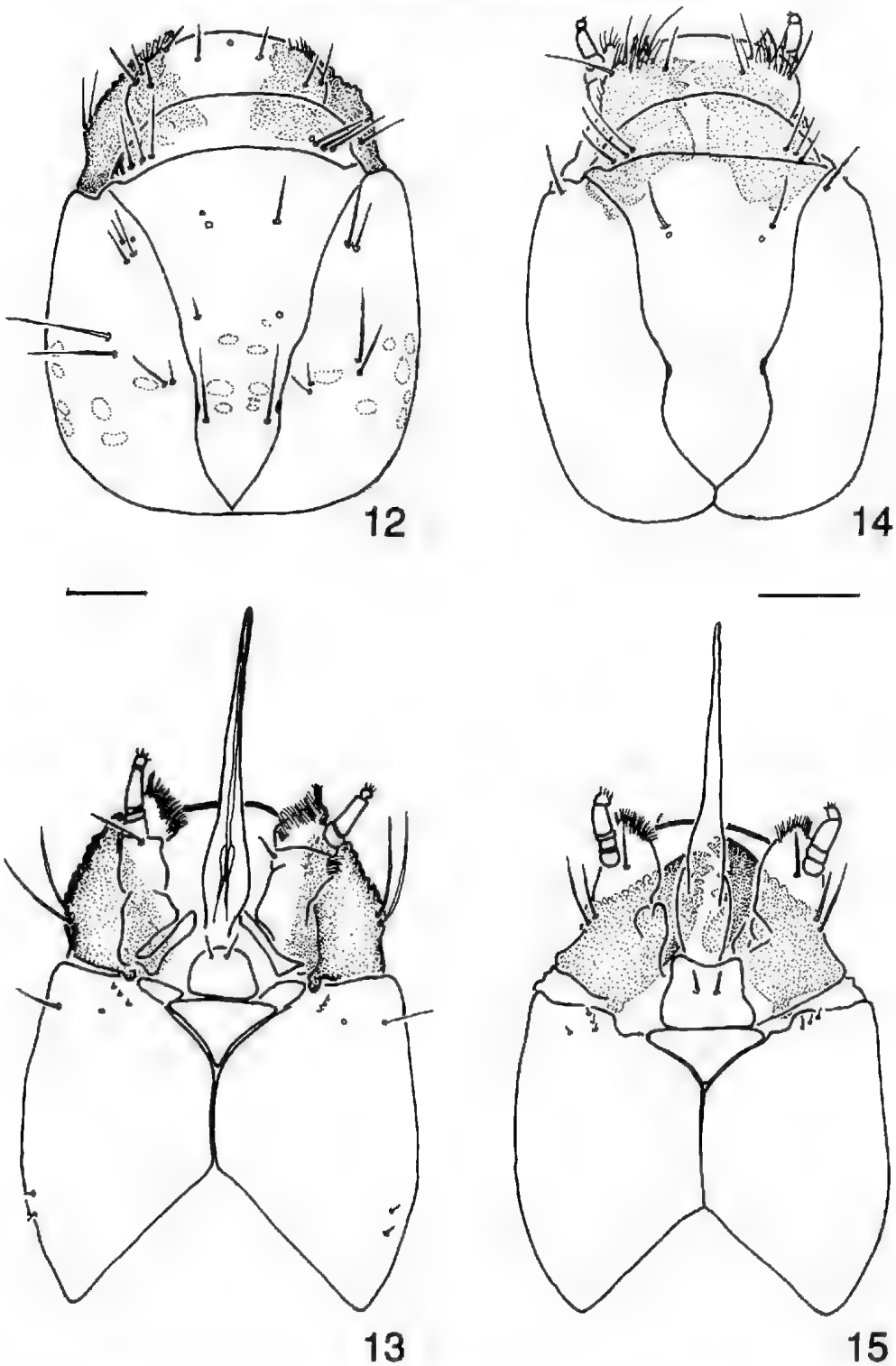
Pupa (Figs 9-11, 21). Length 7.5-10.3 mm. Labrum (Fig. 9) short, with a small marginal papilla apico-mesally. Mandibles (Fig. 10), simple, slender, curved. Hook plates (Fig. 21) with 3-5 denticles, on abdominal segments III-VIII, posterior plates on segment V only, developed into hand-like processes. Posterior abdomen (Fig. 11) divided into two simple setose lobes.

Biology. Larvae and pupae were extracted from fragmented silken tubes. The exact architecture of the larval dwelling is unknown, but the branched portions of tubes appear to have all the features of the tubes of *Phylocentropus placidus* (see Wallace *et al.* 1976) and *P. carolinus* Carpenter (see Wiggins 1977, Fig. 15.4D). (Such features are also shared by *Protodipseudopsis* sp. (un-named) as illustrated by Gibbs (1968, Fig. 3)). The architecture of the *Hyalopsyche disjuncta* dwelling is probably similar: a blunt-ended vertical branch with a small opening projected into the flow, a series of connected cross tunnels, and a dilated net chamber.

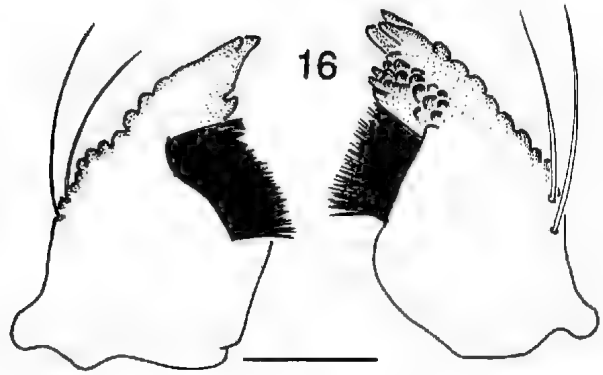
Habitat. Larval tubes were collected from a small stream with a rather unstable base of coarse sand. The dwelling tubes were found attached to logs amongst deeply packed sand and litter, usually in situations where the litter, trapped against logs embedded in the

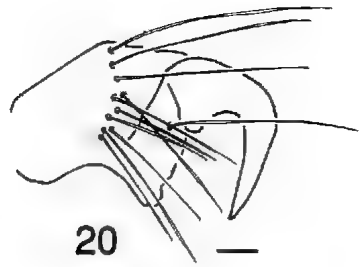


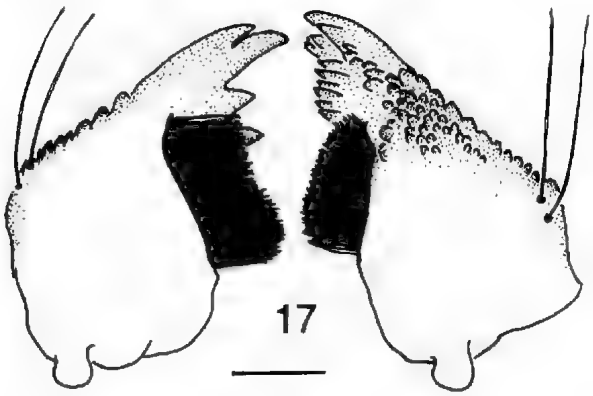
Figs 7-8. *Hyalopsyche disjuncta* Neboiss, larva: 7, whole animal, lateral view; 8, mesosternum.
Figs 9-11. *Hyalopsyche disjuncta* Neboiss, pupa: 9, labrum; 10, mandibles; 11, posterior abdomen.
Scale bars = 1 mm, unless otherwise indicated.

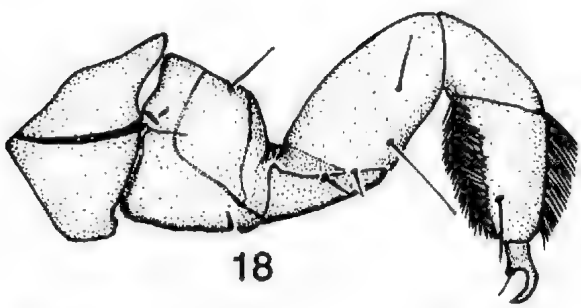


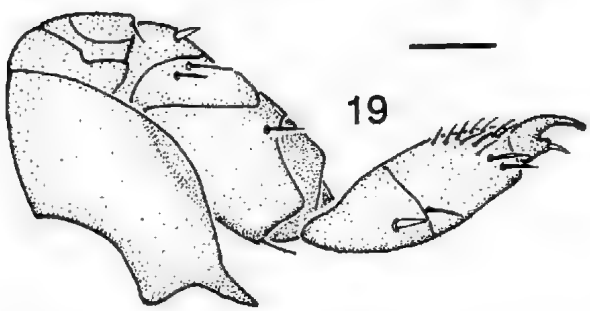
Figs 12, 13. *Hyalopsyche disjuncta* Neboiss, larval head, dorsal and ventral views.
Figs 14, 15. *Phylocentropus* sp., larval head, dorsal and ventral views.
Scale bars = 0.1 mm.











Figs 16, 17. *Hyalopsyche disjuncta* Neboiss and *Phylocentropus* sp., larval mandibles, dorsal view.
Figs 18-20. *Hyalopsyche disjuncta* Neboiss, larva. 18, foreleg and proleuron; 19, midleg; 20, anal proleg.
Fig. 21. *Hyalopsyche disjuncta* Neboiss, pupal hook plates, right side.
Scale bars = 0.1 mm.

sand, was beginning to decompose. Collections of adults were obtained at lights beside small and larger streams; the smaller streams generally were almost completely shaded by the canopies of riparian trees, the larger streams were open.

Discussion

Comparisons of features of larval *Hyalopsyche disjuncta* with those of *Phylocentropus placidus*, *P. lucidus* and *P. carolinus* (from Ross & Gibbs 1973 Fig. 2; Wiggins 1977 Fig. 15.4D; and this work, Figs 14, 15) reveal extraordinarily close similarities between species in the two genera, in derived or specialised features. In general form the heads are similar (compare for example Figs 12, 13 and *Phylocentropus* sp., Figs 14, 15); mandibles of all species are stout, with rugose sculpturing dorsally, albeit on only the right mandible in *H. disjuncta*; ventral sclerites differ slightly, with the submentum of *H. disjuncta* rounded rather than subquadrate; the *lobus internus* of the maxillary palp of *H. disjuncta* is broad and apically truncate rather than tapered and rounded; labia are modified to form virtually identical slender, elongate spinnerets. Thoracic features, too, show close resemblance and the highly specialised legs differ only in the exact shape of the specialised setae adpressed to the mesal margin of the fore tarsi. *H. disjuncta* lacks gills but conforms with *Phylocentropus* species in form of anal prolegs and their claws. The larval niches appear to be identical.

Pupae are relatively uninformative: mandibles of *H. disjuncta* resemble those illustrated by Ross (1944, Fig. 204) for *P. placidus*. Little information is available on pupae of *Phylocentropus*.

Some of the above features occur in other caddis larvae. For example, specialised elongate spinnerets are seen in larvae of some Psychomyiidae and some Ecnomidae, although in these families the spinnerets are proportionally shorter than in *Phylocentropus* and *Hyalopsyche*. Simple anal claws also occur elsewhere, but are probably plesiomorphous. The highly modified, flattened limbs, the form of the mandibles and the larval niche are found only in *Hyalopsyche*, *Phylocentropus*, *Protodipseudopsis* and *Dipseudopsis*.

The probability of such a suite of resemblances evolving by convergence are slim. The simplest hypothesis is that these taxa arose from the same specialised ancestral stock.

Adult characters do not concur with those of the larvae. No clear synapomorphies can be recognised, which is the very reason that placement of these genera has been confused for so long. Among adult features several small differences in general body features can be observed between *Hyalopsyche* and *Phylocentropus*, such as the arrangement of setae on the meta-scutellum (see Figs 2, 5) and the absence of several crossveins in the wings; as well as other more major ones, such as shape of head, position of antennae, reduction of maxillary palpi and form of genitalia. These differences probably represent autapomorphies for the particular genera. The wings of *Hyalopsyche* can be derived from those of *Phylocentropus*, which closely resemble polycentropodid wings, simply by loss of several crossveins; those of *Phylocentropus* probably represent the plesiomorphous form. Similarities such as form of the tentorium (Figs 1, 4) are probably also plesiomorphous.

Superficially, the female genitalia of *Hyalopsyche disjuncta* (Fig. 3) appear to be strikingly different from those of *Phylocentropus placidus* (Fig. 6). Yet upon close examination, similarities are apparent, particularly in the cerci and papillae. Derivation of the *Hyalopsyche* form from that of *Phylocentropus* requires only simple elongation of the arrangement seen in *Phylocentropus*, probably adapting *Hyalopsyche* females for oviposition into sand or crevices. Investigation of the female of *Dipseudopsis indica* McLachlan during this study, indicated that on the basis of female genitalia and wing form, *Phylocentropus* and *Hyalopsyche* are closer than *Dipseudopsis-Hyalopsyche*.

Association of females and larvae of a species in *Hyalopsyche* has helped to stabilise the higher level taxonomy of this genus, placing it in the family Dipseudopsidae. On the basis of studies reported here and examination of the literature, we suggest that *Hyalopsyche* and *Phylocentropus* represent sister groups.

Ross & Gibbs (1973) suggested on the basis of similarities between *Phylocentropus* and Polycentropodinae that *Phylocentropus* is closer to the ancestral stock than other Dipseudopsinae (=Dipseudopsidae) and, given its occurrence in the Oligocene Baltic ambers, they suggested a Eurasian origin for the subfamily (=family). We have not found evidence with which to dispute this contention — the single north-eastern Australian species in *Hyalopsyche* is undoubtedly of Oriental origin. Careful phylogenetic analyses in the future will elucidate intrafamilial relationships, but at last the family Dipseudopsidae is reunited.

Acknowledgments

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Dr J.S. Weaver of the University of New Hampshire, USA, kindly provided material of *Phylocentropus lucidus* and *Dipseudopsis indica* from his collection for comparisons. Adults of *Phylocentropus placidus* and larvae of *Phylocentropus* sp. were made available by Dr J. Morse, on loan from Clemson University, USA.

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OBSERVATIONS ON THE BREEDING BIOLOGY OF A MICROHYLID FROG (GENUS *OREOPHRYNE)* FROM NEW GUINEA

BY G. R. JOHNSTON & S. J. RICHARDS

Summary

Transactions of the Royal Society of S. Aust. (1993), **117**(2), 105-107.

BRIEF COMMUNICATION

OBSERVATIONS ON THE BREEDING BIOLOGY OF A MICROHYLID FROG (GENUS *OREOPHRYNE*) FROM NEW GUINEA

The conquest of terrestrial environments is a major theme in vertebrate evolution. Classically the Amphibia have been viewed as an intermediate stage between the aquatic and terrestrial groups[1,2]. However, the standard view of the amphibian life-cycle involving eggs hatching into aquatic tadpoles which subsequently metamorphose into terrestrial frogs belies the true diversity of reproductive modes in the Amphibia.

The diversity of reproductive modes is greater among amphibians than in other vertebrates[3]. All orders of the Amphibia include species which deposit eggs in terrestrial environments, and terrestrial development has evolved several times within the order Anura[3].

Deposition of eggs out of water is a major step toward terrestriality among amphibians. Therefore, it is not surprising that most variation in reproductive modes among anurans occurs in tropical environments where there are high levels of atmospheric moisture[3]. A second major step toward terrestriality occurs in those groups which exhibit direct development. The evolution of direct development has been important in the successful invasion of montane environments by amphibians[3]. Direct development occurs in all Australopapuan microhylid frogs[4].

Despite their abundance, little is known about the breeding biology of New Guinean microhylids. Small numbers of large, heavily yolked eggs are concealed in leaf axils, hollow stems, moss clumps or beneath the ground[4,5]. They may be attended by an adult frog, usually a male[4,5]. These frogs generally do not form breeding aggregations (exceptions may be *Asterophrys turpicula*[6] and *Sphenophryne mehelyi*[7]) and may call spasmodically. Thus any observations are fortuitous and valuable.

This note reports observations on the reproductive biology of an unidentified species of *Oreophryne* near Tabubil in the Western Province of Papua New Guinea (5°17′S, 141°12′E). This species was assigned to *Oreophryne* on the basis of its partially webbed feet and the presence of small clavicles[8]. Current confusion surrounding the taxonomy of this genus prevents reliable allocation of our specimens to any particular species.

On the evening of 27.xi.1991 a single specimen was found 3.5 km SSW of Tabubil near a small creek, beneath a closed canopy mid-montane rainforest[9]. At the time of collection it was sitting over a clutch of ten eggs on the underside of a leaf 0.8m from the edge of the creek and 1.5m above the ground (Fig. 1). It was not heard calling, but its sex was determined later by dissection. Only two other species of frog were heard calling in the area (*Rana grisea* and an undescribed member of the *Litoria eucnemis* species-group).

The clutch was arranged in two vertical lines of four and six eggs each. The entire clutch was covered with a thin, transparent, membranous structure which yellowed slightly in alcohol. This layer was quite separate from the jelly-like capsule which surrounded the embryos and, although superficially different, may be homologous to the cord that joins the eggs of congeners for which the eggs are known[8,10,11]. The capsules were 3.8-4.0mm in diameter. The

Fig. 1. A male *Oreophryne* (SAM R40884) attending a clutch of eggs on the underside of a leaf near Tabubil, Papua New Guinea.

embryos were 3.7-3.8mm long. Each egg contained a very large, ovoid yolk body 3.1-3.2mm in maximum diameter.

A single egg from this clutch was dissected (Fig. 2). The head (1.1×1.1mm) could be distinguished clearly from the laterally compressed body, which was 2.6mm long. Four limb buds were present, although no differentiation of the digits was apparent. Posterior to the hindlimb buds the tail was strongly compressed laterally, but no vascularisation was apparent in the preserved material. Three cephalic lobes and a pair of pigmented eye spots were clearly visible. A single pair of gill buds were present on each side of the head. Dorsally, two dark lines ran the length of the body, indicating that the neural groove had not yet closed. With the exception of the presence of eye pigmentation and the lack of neural groove closure, these microhylid embryos resemble stage five embryos of the South American leptodactylid, *Eleutherodactylus coqui*[12].

Price[11] illustrated a single, much older embryo of *Oreophryne* from Yapen Island, Irian Jaya. The tail was greatly enlarged and highly vascularised late in development, and presumably plays a role in respiratory gas exchange.

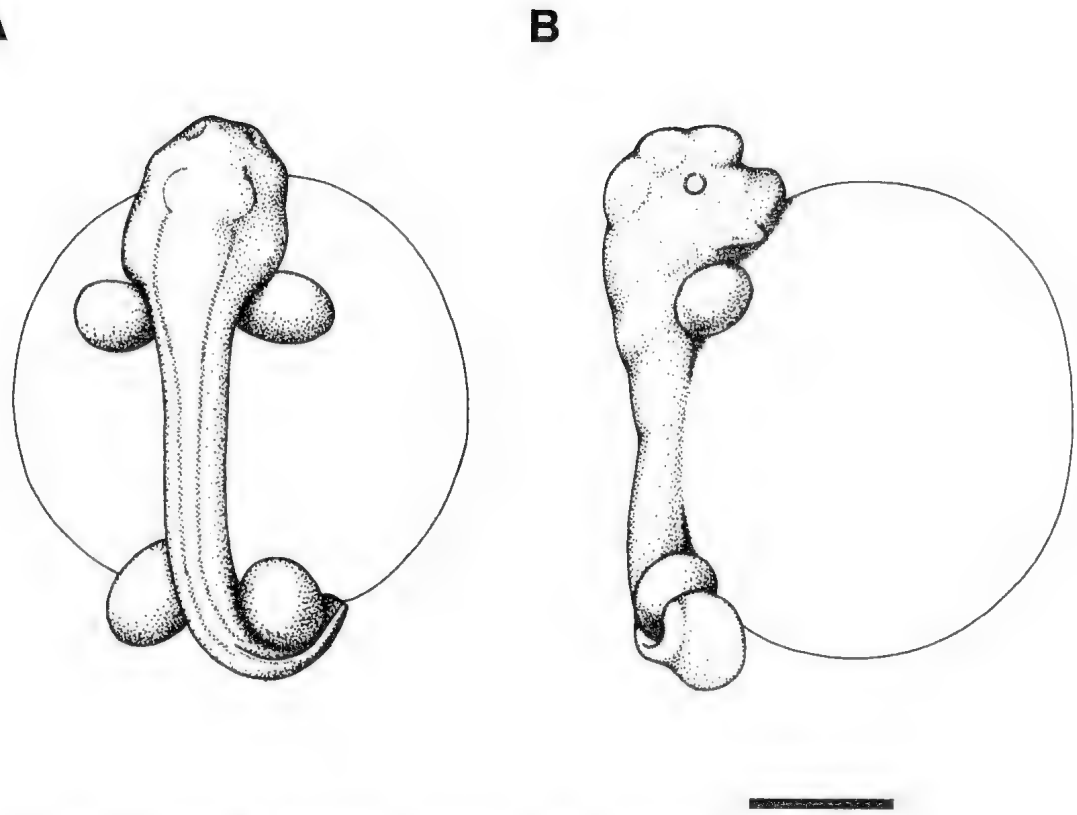

Fig. 2. Dorsal (A) and lateral (B) views of an *Oreophryne* embryo. Scale bar = 1mm.

Measurements of the adult frog were: snout-vent length 22.6mm; head length 7.5mm; head width 7.8mm; eye diameter 3.1mm; eye to naris distance 1.9mm; internarial span 1.8mm; tibia length 10.9mm; foot length 14.2mm. The frog and the clutch it attended have been registered in the South Australian Museum as R40884.

A further two, morphologically identical, male *Oreophryne* were found calling from a cluster of large leaves 3m above the ground, 4m from a sago, swamp amongst mid-montane rainforest 6km SSW of Tabubil at night on 1.xii.1991. Their calls were recorded with a SONY Professional Walkman cassette recorder and an Electret Condenser microphone ECM Z200. Calls were analysed using ULTRASOUND v1.10[13]. The call (Fig. 3) was a biphasic rattle, beginning with a short (0.3-0.4s) series of pulses at 3.2kHz which was followed by a longer (0.7-1.0s) series of pulses at the fundamental and dominant frequency of 2.8kHz, and at 3.2kHz. There were 26 pulses.s^{-1}. Eight calls uttered by two individuals gave a mean call rate of one per 63s. The call length was 1.0-1.4s (mean = 1.1, SD = 0.17).

The breeding behaviour of thirteen of the 83 species of Australopapuan microhylids[14,15,16,17] has been documented[5,10,11,16,18,19,20]. Four to 55 eggs are laid[11]. This reduction in clutch size associated with large, yolked eggs is a common correlate of terrestrial reproduction in amphibians[21].

Males are known to attend eggs in two *Phrynomantis* spp., two *Cophixalus* spp. and three *Sphenophryne* spp.[3,4,18,19] Both males and females attend eggs in two *Oreophryne* spp. and one species of *Cophixalus*[10,20]. Tyler[7] reported aggregations of *Sphenophryne mehelyi* attending their individual clutches of eggs. It is not known how long this association of adult frogs with their clutches may last. The association of frogs with their eggs may function in manipulation of eggs, to provide moisture for terrestrial eggs, in protection against predators or for removal of dead or infected eggs[20].

This report is the first record of any direct developing species laying its eggs on the exposed surface of a leaf. A number of indirect developing frogs from other families are known to deposit eggs on vegetation overhanging water in the neotropics[22,23], Africa[24], Madasgascar[25], the Phillipines[26] and New Guinea[27]. In all of these species the hatching tadpoles fall into the water below. The *Oreophryne* we observed breeding in New Guinea were also found in association with water. This may have been an artefact, however, as we concentrated our searches for frogs around water bodies and did not search the forest surrounding them as thoroughly.

This work was funded in part by grants from the Peter Rankin Trust Fund for Herpetology and the James Cook University. Ok Tedi Mining Ltd, and Phil and Sue Gregory

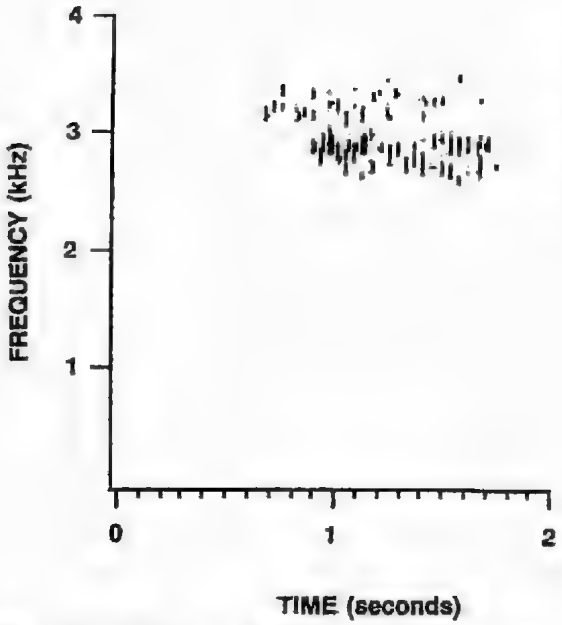

Fig. 3. Sonagram of the call of an *Oreophryne* from 6 km southeast of Tabubil, Papua New Guinea.

assisted with logistic support and transport in New Guinea. Ken Sanderson allowed us to use his software to analyse the call. Nelson Kanem assisted in the field. Margaret Davies and Paula Dempsey made helpful comments on the manuscript. Our work in New Guinea could not have been done without the help of Guy Kula (Department for the Environment, PNG), Rosalyn Busava (Institute of Papua New Guinea Studies) and James Menzies (University of Papua New Guinea).

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THE TADPOLE OF THE AUSTRALOPAPUAN FROG *LITORIA NIGROFRENATA* (GÜNTHER, 1867) (ANURA: HYLIDAE)

BY MICHAEL R. CROSSLAND & STEPHEN J. RICHARDS

Summary

Transactions of the Royal Society of S. Aust. (1993), 117(2), 109-110.

BRIEF COMMUNICATION

THE TADPOLE OF THE AUSTRALOPAPUAN FROG *LITORIA NIGROFRENATA* (GÜNTHER, 1867) (ANURA: HYLIDAE)

The terrestrial hylid frog *Litoria nigrofrenata* occurs in seasonally dry forest and woodland habitats on Cape York Peninsula, the Torres Strait Islands, and in southern New Guinea[1]. Little is known about its biology, and the tadpole is hitherto undescribed. We present observations on breeding activity of adult frogs and describe the tadpole, from Heathlands Reserve between Weipa and Bamaga on Cape York Peninsula (11°45′S, 142°35′E).

Reproductive activity was observed during February and April 1992, when males called from the banks of temporary rain-filled water bodies. None were observed to use elevated calling sites, and all called within 5 m of the water's edge. Oviposition occurred in five cattle watering tanks between December 1991 and February 1992, and tadpoles were also observed in a large (14.4 × 9.6 × 0.5 m) but temporary dam in April 1992. An amplectant pair (male = 38.0 mm SV, female = 46.0 mm SV) collected at the dam on 14.ii.1993 laid 445 eggs in a single clump 2-5 eggs deep. Reproductive activity was not observed during September and November/December 1991 when temporary water bodies were dry. Despite intensive searches, no *L. nigrofrenata* tadpoles were collected from permanent creeks (Cockatoo, Gunshot, Cholmondeley, and Bertie Creeks) or from two permanent swamps during the study, suggesting that this species breeds predominantly in temporary water bodies.

Tadpoles were collected from the dam and watering tanks in April 1992. Tadpoles (n = 288) were collected with a dip net, measured (body length) with vernier calipers, and staged[2]. Some individuals were immediately preserved in 10% formalin. Others were reared to metamorphosis for identification. Preserved specimens were returned to the laboratory and standard measurements[3] were made using vernier calipers (total length and body length) and a dissecting microscope with an optical micrometer (all other measurements). Measurements involving apertures were taken from the centre of the aperture.

Table 1 shows the size distribution of *L. nigrofrenata* at stages 25-39. A tadpole at stage 39 is illustrated in Fig. 1 and has the following dimensions (mm): 43.0 total length, 19.80 body length, 11.72 maximum body width, 11.34 maximum body depth, 4.41 basal tail muscle height, 3.53 basal tail muscle width, 4.54 maximum dorsal fin height located 8.57 from body terminus, 3.91 maximum ventral fin height located 6.30 from body terminus, 3.53 tail muscle height at maximum dorsal fin height, 4.03 tail muscle height at maximum ventral fin height, 4.91 distance between joining of ventral and dorsal fin aspects to body, 10.46 body width at eyes, 10.08 width of outer eye surfaces, 8.19 interorbital distance, 2.90 eye diameter, 1.01 pupil diameter, 0.38 narial diameter, 3.15 internarial distance, 2.39 snout-naris, 5.80 snout-eye, 11.09 snout-spiracle, 5.17 transverse oral disc diameter.

The oral disc of a tadpole at stage 39 is illustrated in Fig. 2. The mouth is anteroventral (almost ventral), and the posterior rim of the labium is strongly folded. The marginal papillae are in two rows anterolaterally and 2-3 rows posteriorly with a narrow gap anteriorly. Submarginal papillae occur in a large patch laterally on the posterior half of the

TABLE 1. *Body length (mm) and Gosner (1960) stage of* Litoria nigrofrenata *tadpoles.*

Stage	N	Mean body length ± SD
25	253	9.80±2.94
26	8	16.74±1.59
27	3	18.97±0.97
28	1	19.00
29	2	17.60±2.12
30	4	19.01±1.17
31	8	19.62±1.36
32	2	19.15±0.64
35	1	20.40
37	1	20.90
38	5	20.86±0.98
39	1	19.80

FIG. 1. Lateral view of a *Litoria nigrofrenata* tadpole in stage 39. Scale bar = 5 mm.

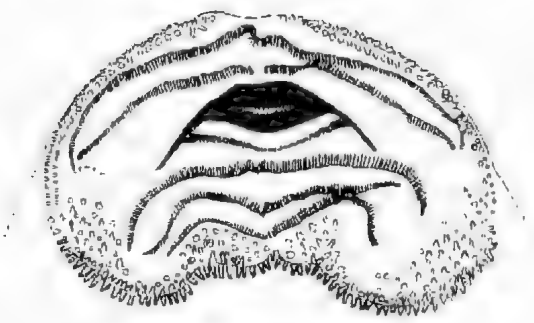

Fig. 2. Oral disc of a *Litoria nigrofrenata* tadpole at stage 39. Scale bar = 1 mm.

labium. The papillae on the anterolateral margins are smaller than those on the posterior margin, and the papillae in the outer row are smaller than those in the inner row. The tooth row formula is 2(2)/3 and the A2 gap is very narrow. One specimen has an additional, poorly developed tooth row located in the anterior gap in the marginal papillae. The keratinised jaw sheaths are narrow and serrated. The upper sheath is broadly curved (medial section almost straight), and the lower sheath is broadly V-shaped. The eyes are large and located dorsolaterally. The nares are dorsal, oriented slightly anterolaterally, and open almost vertically.

The body is oval and rather slender. The fins are high, arched, and terminate in a narrow tip or flagellum. The sinistral spiracle is located ventrolaterally and oriented posterodorsally. The lateral wall is longer than the medial wall and is unpigmented on the posterior two-thirds. The orifice is large, and is clearly visible in dorsal view. The vent tube is short, dextral, attached to the ventral tail fin, and opens 1.3 mm from the tail-body junction.

In life the dorsum is dark brown. A cream stripe runs from the tip of the snout through the top one third of the eye and terminates just posterior to the eye. The ventral surface has a copper pigmentation which extends one-third of the way up the lateral aspect of the body. Posteriorly, three pale stripes extend transversely from the lateral surfaces onto the dorsum, but do not connect dorsally. The pale stripes on the snout and body are most conspicuous in small (stage 25) tadpoles, becoming indistinct in larger animals. The tail fins have a reddish coloration mottled with patches of dark pigment. The copper coloration of the ventral surface, the pale stripes and the reddish tinge of the tail fins disappear in preservative, but the patches of irregular, dark pigment on the tail fins are retained.

The maximum body length attained is 21.15 mm (Stage 38). The SV length of a recently metamorphosed individual (stage 46) was 16.85 mm, and the postocular stripe characteristic of this species was clearly visible.

It has been suggested[4,5] that *Litoria nigrofrenata*, *L. personata* and *L. wotjulumensis* are more closely related to each other than to other Australian frogs. Similarities between the tadpoles of *Litoria wotjulumensis*[6], and *L. nigrofrenata* support that proposed close relationship. *Litoria nigrofrenata* tadpoles share with *L. wotjulumensis* a tooth row formula of 2(2)/3, and arched, heavily mottled tail fins. *L. wotjulumensis* tadpoles apparently lack the patches of submarginal papillae on the lower labium and have a white venter[6] (copper in *nigrofrenata*). The tadpole of *L. personata*[5] differs from *L. nigrofrenata* and *L. wotjulumensis* in having a complete border of marginal papillae, gaps in the P1 and P2 tooth rows, low fins, and distinct gold stripes. The larval morphology of this species does not support a close relationship with the *L. nigrofrenata* species group.

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VOL. 117, PART 3

ROTIFERA FROM AUSTRALIAN INLAND WATERS. IX. GASTROPODIDAE, SYNCHAETIDAE, ASPLANCHNIDAE (ROTIFERA: MONOGONONTA)

BY R. J. SHIEL & W. KOSTE†*

Summary

A brief history of this 12 part series of papers on the Australian Rotifera is given. Of 28 rotifer families, the Australian species of 14 families were revised in the first eight parts. In this part, keys are given to the genera and species of three further families: Gastropodidae *(Gastropus,* three spp.; *Ascomorpha,* three spp), Synchaetidae *(Synchaeta,* ten spp.; *Polyarthra* six spp.; *Ploesoma,* two spp.) and Asplanchnidae *(Asplanchnopus,* two spp.; *Asplanchna,* seven spp.) all of which are planktonic in Australian inland waters. A new species of *Synchaeta* is described from the Fitzroy R., Queensland. All species of these genera recorded from Australian waters are described and figured with known distribution data and ecological information.

KEY WORDS: Rotifera, Monogononta, Gastropodidae, Synchaetidae, *Synchaeta* sp.nov., Asplanchnidae, Australia, descriptions, keys, trophi, biogeography.

Transactions of the Royal Society of S. Aust. (1993), 117(3), 111–139.

ROTIFERA FROM AUSTRALIAN INLAND WATERS. IX. GASTROPODIDAE, SYNCHAETIDAE, ASPLANCHNIDAE (ROTIFERA: MONOGONONTA)

by R. J. SHIEL* & W. KOSTE†

Summary

SHIEL, R. J. & KOSTE, W. (1993) Rotifera from Australian inland waters IX. Gastropodidae, Synchaetidae, Asplanchnidae (Rotifera: Monogononta) *Trans. R. Soc. S. Aust.* 117(3), 111–139, 30 November, 1993.

A brief history of this 12 part series of papers on the Australian Rotifera is given. Of 28 rotifer families, the Australian species of 14 families were revised in the first eight parts. In this part, keys are given to the genera and species of three further families: Gastropodidae (*Gastropus*, three spp.; *Ascomorpha*, three spp), Synchaetidae (*Synchaeta*, ten spp.; *Polyarthra* six spp.; *Ploesoma*, two spp.) and Asplanchnidae (*Asplanchnopus*, two spp.; *Asplanchna*, seven spp.) all of which are planktonic in Australian inland waters. A new species of *Synchaeta* is described from the Fitzroy R., Queensland. All species of these genera recorded from Australian waters are described and figured with known distribution data and ecological information.

KEY WORDS: Rotifera, Monogononta, Gastropodidae, Synchaetidae, *Synchaeta* sp.nov., Asplanchnidae, Australia, descriptions, keys, trophi, biogeography.

Introduction

An earlier paper (Shiel & Koste 1979) collated the known records of Australian Rotifera from a widely scattered literature. At that time, 331 taxa were recognized from inland waters of the continent. Thereafter we proposed to accumulate additional records for publication as short checklists, with descriptions of new taxa as they occurred (e.g. Koste & Shiel 1980). Our own samples accrued, and widely separated colleagues sent material from various parts of the mainland and Tasmania. Many of the rotifers we found could not be identified from the keys of Kutikova (1970) or Koste (1978a), the recognized authorities. Rotifers generally were considered cosmopolitan at that time, however, our samples indicated that the Australian rotifer fauna contained a distinct indigenous component. Taxonomic keys to them simply were not available, so to provide such keys became our aim.

The probable audience for a taxonomic volume on Australian rotifers comparable to the revision by Koste (1978a) was considered too small to bear the production cost. Further, WK had taken some 12 years to complete the European revision, and the prospect of another 12 on the Australian fauna was daunting. A series of smaller "manageable" papers seemed to be appropriate to put keys to species in the hands of the scattered collectors. We therefore started to draft keys to the common planktonic species in May 1984 (WK was then 72), working by family or groups of families.

The Editor of the CSIRO journals was approached, and agreed to take the first manuscript, on bdelloid rotifers occasionally found in plankton. This was published in *The Australian Journal of Marine and Freshwater Research* (Koste & Shiel 1986). The following year, the second paper of the series (the monogonont families Epiphanidae and Brachionidae) was published in a new CSIRO journal, *Invertebrate Taxonomy* (Koste & Shiel 1987a). Then followed a hiatus when papers III and IV were "lost" in the system in 1987-88 and subsequently withdrawn, without rancour, from *Invert. Taxon.* To keep the series in Australia we approached the Editor of the *Transactions of the Royal Society of South Australia*, were accepted, and saw the Euchlanidae, Mytilinidae, Trichotriidae and Colurellidae appear in 1989 (Koste & Shiel 1989a, b). Subsequently, Lecanidae, Proalidae and Lindiidae (Koste & Shiel 1990a, b), Notommatidae (Koste & Shiel 1991) and Trichocercidae (Shiel & Koste 1992) have continued the series.

In the interim, the contents were expanded to include all known Australian rotifers, not only pelagic taxa. The littoral taxa are considerably more diverse, and determining whether some of them were in fact what they were named has been a slow process. The need for a complete global revision of rotifer systematics compounded our difficulties. We apologize for the rate-decrease, but plead that demands on both of us are greater as more researchers become interested in the Rotifera, and seek assistance. WK bears the weight of the global community of rotifer workers; RJS has only Australasia to deal with, hence has taken over production of the series, and is responsible for errors or omissions which may sneak through.

So, for those avid readers who have agitated for keys to the families yet to appear, the end is in sight! Three further families are reviewed in this part (Gastropodidae, Synchaetidae, Asplanchnidae). Two remaining ploimate families (Dicranophoridae, Microcodinidae,

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32 spp., part X) should be completed early in 1994, and the eight families of Flosculariacea (73 spp., part XI) and Collothecacea (16 spp., part XII) during 1994. By this time a global systematic revision now in preparation should be available, and the confused status of some of the taxa in our earlier parts be resolved (see also Biogeography section later). The first and introductory volume has been published (Nogrady *et al.* 1993) and the systematic sections will be published in parts by family. For recent research on rotifers, see also Gilbert *et al.* (1993).

The three families reviewed here contain about 33 species, all more or less exclusively pelagic in habit. They are less diverse than other common pelagic families, e.g. Brachionidae or Trichocercidae, both with >45 taxa recorded (Koste & Shiel 1987a; Shiel & Koste 1992), but species of Gastropodidae and Synchaetidae appear to be numerically the most common planktors in Australian inland waters. Species from the three families occur in virtually any standing freshwaters, where they may reach very high densities, e.g. in Nov. 1981 >24,000 *Synchaeta* spp. l^{-1} occurred in Mt Bold Reservoir, S.A.. (Shiel *et al.* 1987). This represents a significant biomass, even though individual animals are small (most <200 μm). The same study reported sequential *Synchaeta* species replacements (five taxa) in the filling Dartmouth Reservoir (1978-80), but otherwise rotifer limnoplankton composition and community succession is poorly documented in Australia.

Billabongs in particular may support a diverse assemblage of species at any time, with two or more taxa from each family co-occurring. Temporal succession in response to seasonal changes in physico-chemical and biological conditions may be very rapid, e.g. in a billabong near Wodonga, species dominants changed within days in an autumn series of daily plankton samples (Tan & Shiel 1993). In the gastropodids and synchaetids, high population densities, combined with specialized feeding habits, produce profound grazing effects on preferred bacterial/algal populations. In contrast, asplanchnids do not reach such high densities, but may be significant predators in their aquatic food webs, taking other rotifers and microcrustaceans. Species of *Asplanchna* may be the largest predatory zooplankters (>2500 μm) in some habitats. Details of feeding preferences are given in the systematic section.

We stress that it is very likely that undescribed taxa of these rotifer families occur in Australia. More than 50% of the species in some of the genera we have reviewed to date are indigenous, yet only a single asplanchnid and a single synchaetid described here apparently are endemic. While this disparity may be real, it also may reflect a poor level of taxonomic discrimination in earlier studies, i.e. a tendency to 'shoehorn' taxa into the nearest described species. The forthcoming global revision will resolve many of the extant anomalies. For a critique of some problems pertaining to Australian microfauna see Green & Shiel (1992).

In this review the format of earlier parts is followed; for convenience, genera and species are treated alphabetically. Keys to rotifer families are included in Koste & Shiel (1987a), which also contains brief descriptions of general morphology. A family level key in Wallace & Snell (1991) also may be useful. Known distribution and ecological information are given for the species we have encountered. Global distribution and ecology is given in Koste (1978a). Type material generally was not designated in many early studies, nor type localities given. We have included type locality if it is known, otherwise probable place of origin is given in parentheses. Some early authors did not specify origin of material, however we consider it likely that in the late 18th-early 19th century their collections derived from reasonably close to home.

Methods

In living material, the rotifers reviewed here are placed readily into their appropriate families and genera by their characteristic body morphology (Fig. 1). Gastropodidae (*Ascomorpha*, *Gastropus*) (Fig 1:1, 1:2) are ovate-globular with firm cuticular loricae, and distinctive dark 'defaecation vesicles' or coloured chromatophores in the stomach wall. Synchaetidae (*Synchaeta*, *Polyarthra*, *Ploesoma*) (Fig 1:3, 1:4, 1:5) are more varied; *Synchaeta* species are illoricate, pyriform or conical with distinctive anterolateral ciliated auricles (Fig. 1:3a). *Polyarthra* species are small cubes with dorsolateral and dorsoventral foliate appendages (Fig. 1:4a); *Ploesoma* is firmly loricate, with distinctive delineation of the lorica, and relatively large foot (Fig. 1:5a). Asplanchnids (*Asplanchnopus*, *Asplanchna*) are large saccate forms (to 2.5 mm) with large pincer-like incudate trophi. Asplanchnids are superficially similar to, and likely to be confused with large saccate epiphanids (*Epiphanes*) (cf. Koste & Shiel 1987a), with which they may co-occur.

Preservation in alcohol, formalin, gluteraldehyde, etc., induces strong contraction of illoricate saccate forms, or retraction of anterolateral auricles in synchaetids. Resolution of species in the case of strongly contracted animals requires clearing in hypochlorite (NaOCl) and examination of the sclerotized mastax elements — the **trophus**. Trophi are generically distinctive; indeed, evidence to date suggests that they are species specific. Specific determination is more difficult for those taxa with small membraneous trophi, e.g. synchaetids, than for taxa with large heavily sclerotized trophi, e.g. asplanchnids. The difficulty of identifying preserved *Synchaeta* spp., for example, was discussed by Ruttner-Kolisko (1974). Details of trophi preparation for light- and electron

microscopy are given in Koste & Shiel (1989c) and Sanoamuang & McKenzie (1993). Particular care must be taken with *Synchaeta* and *Polyarthra* species; with prolonged immersion, NaOCl is likely to erode delicate trophi. Rapid replacement of NaOCl with non-corrosive mountant (e.g. 10% glycerol-H_2O) is necessary.

A useful pictorial method has resulted from developments in computer software and videography. High resolution 'videographs' approaching light-micrograph quality can be achieved electronically for reasonable cost. The advantages include immediacy, electronic storage, and ability to print black and white or coloured images on a range of laser- or video printers. Several of the photographs in this part were printed using a Sony CVP-G700 printer via a microscope-mounted Sony DXC-107AP video camera. Electronic images also may be captured by a frame-grabber and printed via a laser printer. The resolution on a 600 dpi printer approaches black and white photograph quality. The main advantage here is immediacy. Samples received for identification can be checked, and some or all taxa "grabbed" onto disk storage. An electronic reference collection can be built up, disks can be exchanged much more readily than bottle samples, and printed images can be returned to collectors for the cost of a photocopy.

Systematic section

Rotifer classification has been based largely on morphology, and only in the past decade or so have there been advances in comparative biochemical and ultrastructural methods, e.g. electrophoresis, restriction fragment polymorphism, polymerase chain reactions, SEM, TEM (Koste & Shiel 1989c; Nogrady *et al* 1993).

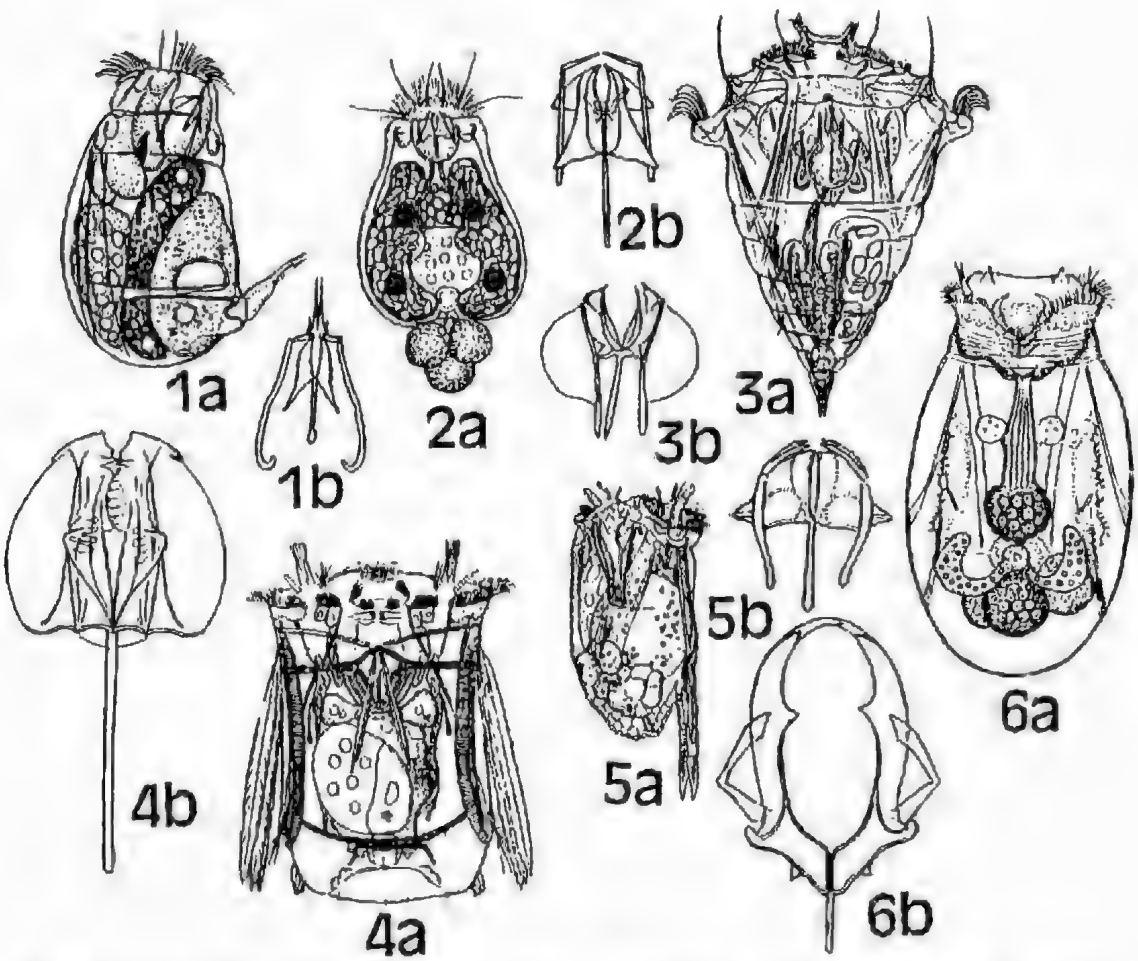


Fig. 1. Habit (a) and trophus morphology (b) of: 1, *Gastropus*; 2, *Ascomorpha*; 3, *Synchaeta*; 4, *Polyarthra*; 5, *Ploesoma*; 6, *Asplanchna*. After Koste (1978a).

These methods will resolve some of the problems observed with morphological criteria, but they are not readily available to the majority of workers. While there are still few workers globally with the necessary expertise, morphology will continue to be the principle classification tool.

The classification followed here is that detailed in Koste & Shiel (1987a) based on the revision by Koste (1978a). This also is the classification used by Wallace & Snell (1991) and Nogrady *et al.* (1993), except that both these works follow the American practice of regarding the Rotifera as a Phylum rather than a Class of the Phylum Aschelminthes. A new classification system based solely on trophi structure has been proposed by Markevich (1990). If ultimately accepted as better than the classical system, it will not affect the specific, generic or familial placement of the Australian rotifer fauna, but will change the placement above family.

Taxonomic descriptions of all the species treated here are after the revision of Koste (1978a). Some taxa have additional descriptive material from the original authors where we felt it was needed. In some cases further description has been added from the Australian material where we were confident that the taxon was the same as the nominate species, but for which the original description was inadequate by modern standards. In some cases the original description lacked figures, trophus details, etc. We have tried to provide figures of general morphology, and to include trophi where possible, but the process is fraught with difficulty when there is doubt that the Australia taxon is the nominate species. In such cases we have included a comment.

Abbreviations for morphometric measurements: BH=body height; BL=body length; BH=body width; FT=foot; F=fin; FL=fin length; FU=fulcrum; FW=fin width; M=manubrium; ME= male egg; R=ramus; RE=resting egg; SE=subitaneous egg; T=toe length; TR=trophi length; TL=total length; U=uncus. All measurements refer to adult females unless otherwise noted.

Family Gastropodidae Remane, 1933

Gastropodids are small, usually highly coloured rotifers common in inland waters Australia-wide. They are characteristically fast swimmers, abundant in spring in the pelagic of reservoirs and billabongs, also in slow reaches of rivers (Shiel *et al.* 1982; Kobayashi & Shiel, in press). Two genera, *Gastropus*, with three spp. known and *Ascomorpha*, with six spp. known globally (Koste 1978a). Three species of each have been recorded from Australia. It is not unusual to find more than one species of each genus co-occurring. In this event there is often a size difference in the congeners, apparently to utilize different resources. Features: rarely semiplanktonic; oval, saccate or flask-shaped; laterally flattened; foot present (*Gastropus*) or absent (*Ascomorpha*); apical field has tentacles in some species; mastax virgate, in *Gastropus* with prepharyngeal cuticular tube; stomach lobed or with blind sacs.

Key to genera

1. Foot absent, 1-4 dark brown to black defaecation (=accretion) vesicles ..... *Ascomorpha* Perty
   Foot present, one or two toes; no dark vesicles ..... *Gastropus* Imhof

Ascomorpha Perty

Ascomorpha Perty 1850: 18.

Type: Ascomorpha ecaudis Perty 1850, p.18.

Body saccate or ovoid, may be dorso-ventrally compressed, lacks foot; cuticle thin, lightly stiffened or with dorsal and ventral plate (*A. ovalis*); apical field with membranelles, ciliary bundles, styli, palpar organs, fingerlike tentacle used for holding prey cells; trophi virgate; unci thin, stiletto-like; rami long, acute, elongate, right-angled dorsally (straight in *A. ovalis*); stomach large (lobed or blind sacs), filling almost entire body; intestine, cloaca and anus absent, wastes stored in 1-4 defaecation or accretion vesicles; large protonephridial bladder present; one cerebral eyespot, displaced to left in *A. ecaudis* and *A. saltans*; dorsal and lateral antennae very small, difficult to see.

Ascomorpha species feed by sucking chromatophores and cell contents from algal cells, or ingesting whole cells. These may be incorporated into the stomach wall, where they may survive and divide, before being digested.

Key to species of *Ascomorpha* Perty known from Australia

1. Corona with finger-like palpar organ (Fig. 2a, 3a) ... 2
   Palpar organ absent (Fig. 1a) ..... *A. ecaudis* Perty
2. Lorica with distinct dorsal and ventral plate ..... *A. ovalis* (Bergendal)
   Stiffened cuticle may have striae, but no distinct plates ..... *A. saltans* Bartsch

Ascomorpha ecaudis Perty
FIG. 2:1

Ascomorpha ecaudis Perty, 1850, p. 18.
Sacculus viridis Gosse, 1851, p. 158.

Type locality: (Switzerland).

Description: Saccate body widest in distal third; cuticle not striated; apical field with ciliary tufts and elongate styli; stomach lobulate with yellow/green/brown contents; four lobes with dark defaecation vesicles, darker in older animals; vitellarium with eight nuclei. Trophi: rami acute, elongate, with triangular alulae (Fig. 2:1b); manubria well developed, fenestrated, terminally straight or slightly curved; 1-2 SE carried attached to cloacal opening; RE spinulate.

TL 130-200 μm; TR 35 μm (FU 17; R 18; M 14)
Distribution: Perennial in plankton of ponds and lakes, often with spring/autumn peaks. Probably pancontinental, but not yet recorded from W.A. Abundant in R. Murray billabongs, also in lower R. Murray plankton in summer (Shiel *et al.* 1982): 8.0-29.8 °C, pH 4.3-7.8, DO 5.8-11.2 mg l^{-1}, 16-551 μS cm^{-1}, 6.8-40.0 NTU, alk. 1.9 mg l^{-1}, TDS 24.9 ppm.

Ascomorpha ovalis (Bergendal)
FIG. 2:2

Anapus ovalis Bergendal, 1892, p. 1.
Ascomorpha ovalis: Carlin 1943, p. 34.

Type locality: (Greenland).
Description: Lorica consists of distinct dorsal and ventral oval plates covered with thin membrane (Fig.

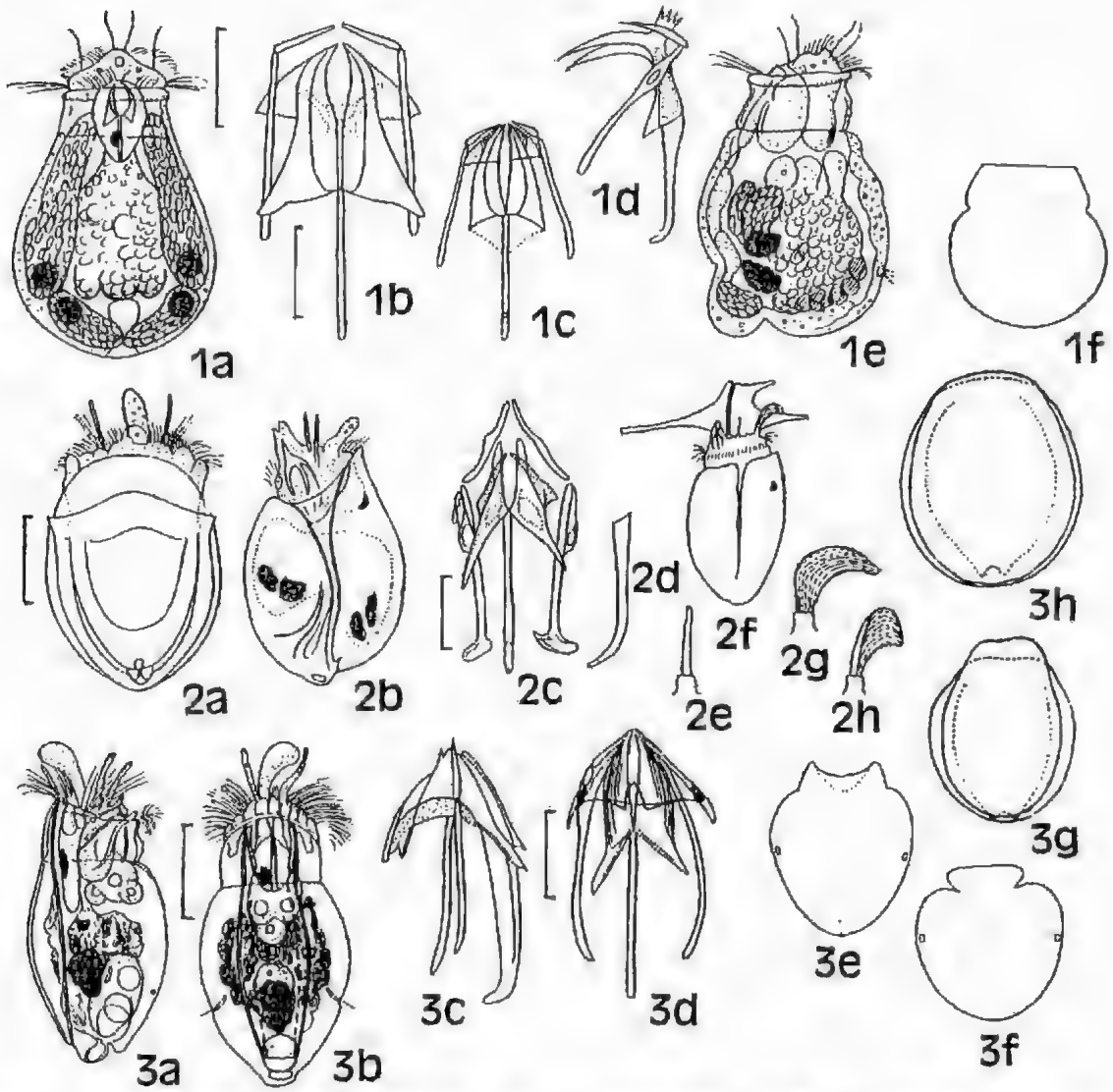


Fig. 2. 1, *Ascomorpha ecaudis* Perty: (a) ventral; (b,c) trophus; (d) trophus, lateral; (e) lateral; (f) body section. 2, *A. ovalis* (Bergendal): (a) ventral; (b) lateral; (c) trophus; (d) fulcrum, lateral; (e) sensilla; (f) using tentacle to hold *Ceratium*; (g,h) tentacle or palpar organ. 3, *A. saltans* Bartsch: (a) lateral; (b) dorsal; (c) trophus, lateral; (d) trophus; (e,f) body sections; (g,h) morphs from different populations. 1f after Donner (1943), (1a-e, 2, 3 after Wulfert (1960)). Scale bars: adults 50 μm, trophi 10 μm.

2:2a, b), apical field with single main tentacle and smaller accessory palpar organ; median red cerebral eye; dorsal antenna small, lateral antenna not reported. Trophi of simple structure: rami occasionally asymmetric, with long alulae; two suprarami above them; unci long, thin rods; manubria distally double-crooked (Fig. 2:2c); stomach with four blind sacs; wastes accumulate as dark irregular balls (generally four); RE spherical, covered with small 'warts'.

TL 100-200 μm; male 70-80 μm, TR 35 μm (FU 20, M 20, U 14); RE 64×60 μm; MT 44×40 μm.

Distribution: Common in plankton, particularly during *Peridinium* or *Ceratium* blooms. *A. ovalis* grasps dinoflagellate cells with its tentacle (Fig. 2:2f), bores through the cell wall with the unci, and uses the mastax as a pump to suck out the cell contents. Chromatophores are digested intracellularly in the stomach wall, which is brownish-yellow as a consequence. Known from N.S.W., N.T., Qld, Tas. & Vic. 14.0-26.0 °C, pH 6.2-7.8, DO 8-9.4 mg l^{-1}, 35-190 μS cm^{-1}, 1-120 NTU.

Ascomorpha saltans Bartsch
FIG. 2:3

Ascomorpha saltans Bartsch, 1870, p. 364

Type locality: 'bei Tübingen', Germany.

Description: Body oval, cuticle stiffened; dorsum with raised, flattened central section between parallel grooves (Fig. 2:3g); head with many folds in contracted individual; apical tentacle commonly deflected dorsally, with two adjacent unusually long stylii (Fig. 2:3a, b); two bundles of stiff bristles form fine tubes each side of mouth; mastax with 2-3 salivary glands; stomach not lobulate; gastric glands not described. Trophi: rami with alulae and domed suprarami; manubria rod-shaped; fulcrum curved dorsally at distal end. Ganglion with red eyespot (displaced to left); elongated retrocerebral sac behind ganglion; protonephridia with ca. 3 flame cells; SE and RE smooth; male undescribed.

TL 100-165 μm; BW to 85 μm; height to 88 μm; TR 28-34 μm.

Distribution: ?Pancontinental, not yet recorded from S.A. Summer occurrence in Murray-Darling reservoirs, e.g. L. Burrinjuck. 12.0-27.0 °C, pH 5.4-7.6, DO 5.8-8.0 mg l^{-1}, 59-1900 μS cm^{-1}, 1-10 NTU.

Comment: A single record of *A. saltans indica* from L. Barracoota, Vic. (Berzins 1982) is unverified. Smaller than the typical form (63-68 μm in contracted individuals), this Indian form has no appreciable trophi differences from *A. saltans* and is here considered an ecotypic variant.

Gastropus Imhof
Gastropus Imhof, 1891, p. 37.

Body laterally compressed; cuticle stiffened; anterior margin undulate; corona a simple band of cilia, may have palps and ciliary bundles within the paracingulum; hypodermis thickened, may have secretory function, e.g. gelatinous sheath in *G. stylifer*; dorsal antenna displaced caudally; lateral antennae asymmetric, difficult to see; mastax with prepharyngeal tube (Fig. 3b, c); trophi virgate; rami stiletto-like or with multi-toothed forked apices; stomach saccate, contains oil droplets and coloured dietary items; as in *Ascomorpha*, cells of stomach wall coloured green or brown by intracellular ingested chromatophores; rectum reduced; anus barely visible, probably non-functional; vitellarium with 8-24 nuclei; foot distinctly annulated, inserted ventrally; single fused toe or two short acute toes. Males with rudimentary digestive tract, evertible penis, relatively large brain with conspicuous cerebral eye. Finely spinulate eggs are attached to pelagic algae; RE with short spines on outer shell. All three described species are recorded from Australia. All are herbivorous. Their trophi pierce algal cells, particularly phytoflagellates. The mastax acts as suction pump through the prepharyngeal tube.

Key to species of Gastropus

1. Foot posteroventral with two toes ..*G. stylifer* Imhof
   Foot mediowentral with single toe 2
2(1). Anterior elongated (Fig. 2a); occipital margin undulating ..... *G. minor* (Rousselet)
   Head not elongated, occipital margin smooth ..... *G. hyptopus* (Ehrenberg)

Gastropus hyptopus (Ehrenberg)
FIG. 3:1

Notommata hyptopus Ehrenberg, 1838, p. 426, Fig. 50:6.
Gastropus hyptopus: Weber, 1898, p. 752

Type locality: 'Bei Berlin', Germany.

Description: Body transparent; anterior cuticle stiffened, not tapered and elongated, with longitudinal furrows; dorsally a short keel; foot short, 2-segmented in adults; stomach with large oil droplets, contents mostly yellowish; brain with large dorsal cerebral eye; vitellarium with many nuclei. Trophi: rami apices with five prongs (Fig. 3:1e); large semicircular alulae on inner margin of manubria; males known; RE spiny (Fig. 3:1g).

TL 150-363 μm; T 25-30 μm; male 60-90 μm; TR 30-37 μm (FU 14 μm, M 15 μm).

Distribution: Widely distributed in eastern Australia, from Qld to Tas., generally in smaller waters, e.g. billabongs or stock dams. Apparently a wider thermal tolerance here than in Europe, where it is reputed as a winter form. 8.0-23.5 °C, DO 4.1-10.8 mg l^{-1}, pH 4.4-7.1, 17-240 μS cm^{-1}, 5-120 NTU.

Literature: Evans (1951), Green (1981), Russell (1961).

Gastropus minor (Rousselet)
FIG. 3:2

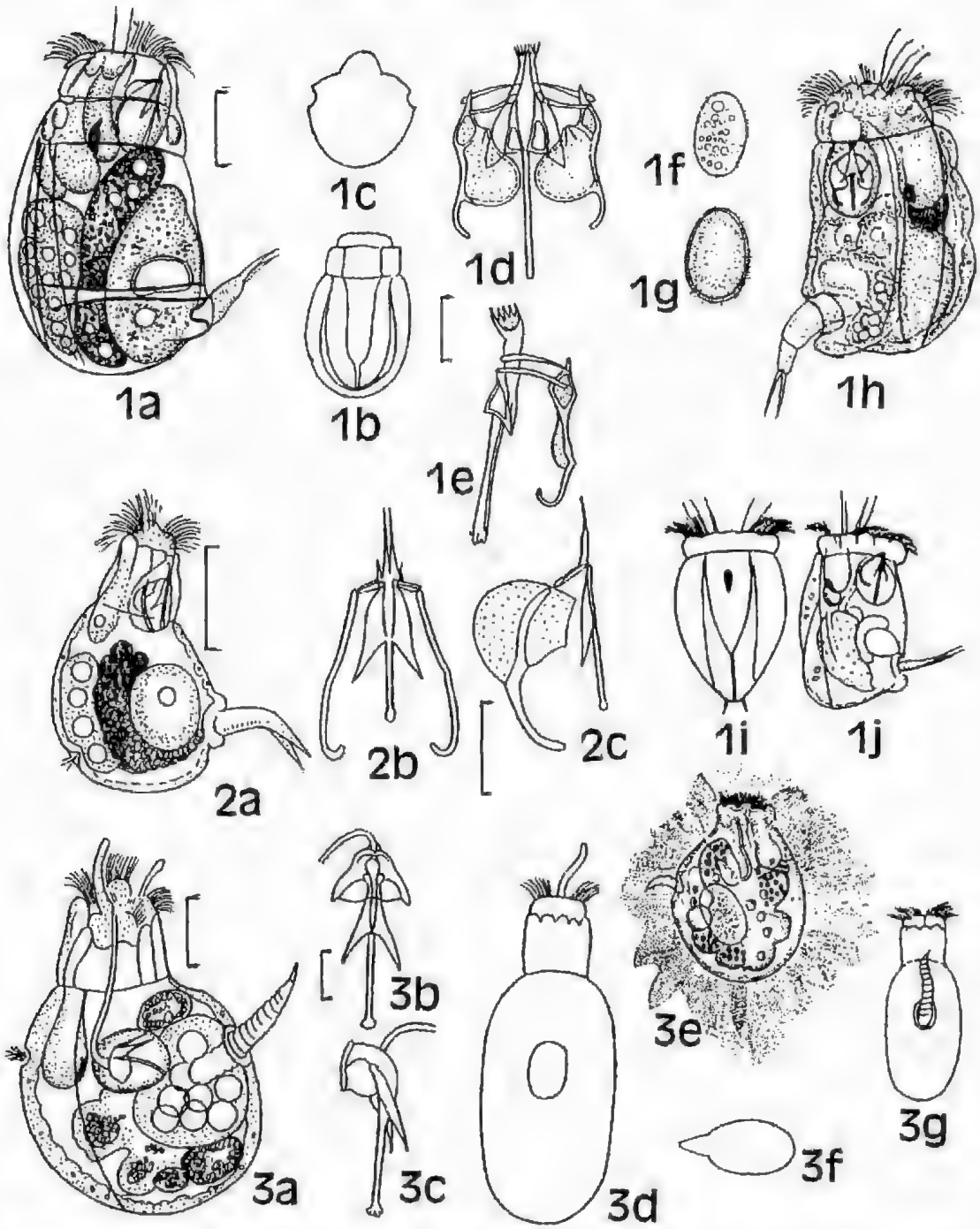


Fig. 3. 1, *Gastropus hyptopus* (Ehrenberg): (a) lateral. (b) lorica with striae: (c) body section: (d) trophus: (e) trophus, lateral: (f) male egg: (g) resting egg: (h) another individual, lateral: (i,j) dorsal and lateral views from another population. 2, *G. minor* (Rousselet): (a) lateral: (b) trophus: (c) trophus, lateral. 3, *G. stylifer* (Imhof): (a) lateral: (b) trophus: (c) trophus, lateral: (d) ventral: (e) animal in gelatinous sheath; (f) body section; (g) ventral with foot extended. 1a-e, h, 2, 3 after Wulfert (1960). 1f, g after Nipkow (1961). Scale bars: adults 50 μm, trophi 10 μm.

Notops minor Rousselet, 1892, p. 359, Fig. 24:9-10.
Gastropus minor: Weber 1898, p. 752.

Type locality: (Europe).
Description: Head tapered, elongate; foot smooth, slightly elongated. Trophi: needle-like rami can be protruded through mouth (Fig. 3:2b); long pointed alulae, almost symmetrical, at rami bases; single unci; manubria bilaterally lamellate (asymmetrical), with sweeping curve to distal crook; fulcrum rodlike. Animal generally colourless, although stomach contents may be brown and contain oil droplets; 4-8 nuclei in vitellarium.

BL 82-140 μm; FT 35 μm; T 20-23 μm; TR 24-30 μm.
Distribution: Known from Qld., N.S.W., N.T., Tas. in small lentic waters, with a single record from the Hopkins R. estuary, Vic.: 8.0-22.0°C, pH 4.9-7.7, 14-60 μS cm^{-1}, <10 NTU.
Literature: Shiel & Koste (1979), Koste (1981).

Gastropus stylifer Imhof
FIG. 3:3

Gastropus stylifer Imhof, 1891, p. 37.
See Koste (1978a) for extensive synonymy.

Type locality: Black Forest, Germany.
Description: Notably brightly coloured; hypodermis blue, body fluid pink; gut contents green/brown; red cerebral eye; occipital margin undulate; with longitudinal striae; raised keel in cross-section; vitellarium with 6-8 nuclei. Trophi: thin, long fulcrum; rami with long pointed alulae; manubria and unci apparently fused into a cup-shape (Fig. 3:3b); long curved prepharyngeal tube present; SE almost smooth; RE warty.

TL 220-250 μm; W 56-70 μm; FT 40 μm; SE 60×40 μm; RE 60×44 μm; male 80 μm; newly-hatched juveniles 75-100 μm.
Distribution: Lays eggs in colonial phytoflagellates (*Dinobryon*, *Uroglena*); feeds on *Peridinium* and other Dynophyceae, sucking out contents (Koste 1978). Most common species of the genus in our collections, occasionally co-occurring with *G. hyptopus*: 9-26°C, pH 4.3-7.6, DO 4.1-10.7 mg l^{-1}, 13-490 μS cm^{-1}, 5-120 NTU.

Family Synchaetidae Remane, 1933

Soft cuticled to more or less loricate; body conical, pyriform, cup-, bell-shaped, vasiform or saccate; corona of *Asplanchna* type with or without ciliary auricles; rigid bristles near mouth; elongate coronal sensillae curve inwards; mastax virgate with complex paired hypopharynx muscles; manubria closely associated with margin of pumping chamber; foot and toes present, rudimentary or absent. Of four described genera, *Ploesoma*, *Polyarthra* and *Synchaeta* are known from Australia; *Pseudoploesoma* is not.

Key to genera

1. Illoricate body, cuticle thin but maintains shape; corona with lateral ciliary auricles; foot more or less distinct with two short toes, occasionally one ..... *Synchaeta* Ehrenberg
   Auricles absent 2
2(1). Body illoricate, saccate-cuboidal; cuticle thin but rigid; foot absent; lateral bundles of rigid serrated fins ..... *Polyarthra* Ehrenberg
   Body loricate, generally with ornamented surfaces (ridges, fillets, etc); foot-opening or ventral aperture present; foot annular and distinct, two toes ..... *Ploesoma* Herrick

Ploesoma Herrick
Ploesoma Herrick, 1885, p. 57.

Body bean-shaped/saccate, distinctly loricate, variously ornamented: dorsal lorica anterior may have headshield, smooth or denticulate margin; ventral lorica closed, with foot-opening, or open with ventral aperture; foot in part or entirely annulate, with robust toes; corona of *Asplanchna* type, with two long digitiform palps in apical field; dorsal antenna displaced caudally; lateral antennae ventral in last third of body; mastax virgate, large; can be extruded to grasp food items; oesophagus long, with longitudinal striae; stomach in distal third of body. Of 7-8 species listed in Koste (1978a), two are recorded from Australia. All known species are planktonic or semiplanktonic carnivores, eating pelagic and benthic rotifers. Cannibalism is noted (Koste 1982).

Key to species of Ploesoma recorded from Australia

Anterior margin of headshield smooth, straight to undulate ..... *P. truncata* (Levander)
Headshield margin with median, short, triangular toothlike extension ..... *P. lenticulare* Herrick

Ploesoma lenticulare Herrick
FIG. 4:1

Ploesoma lenticulare Herrick, 1885, p. 57, Fig. 3a-b.
For extensive synonymy, see Koste (1978a).

Type locality: (U.S.A.).
Description: Occipital margin with smoothly rounded projection; lorica outline variable within and between populations; dorsal transverse furrow contains opening of dorsal antenna; three longitudinal furrows between this median furrow and occipital margin; extensive ornamentation as in Fig. 4:1a; lorica surface covered with small round knobs; ventral lorica with deep cup-shaped aperture; apical field with two digitiform palps, membranelles and sensillae. Trophi: fulcrum long, planklike in lateral view; rami without inner dentition, with large basal plates; manubria with lamellae, unci with two main teeth and striated plate. Male unknown.

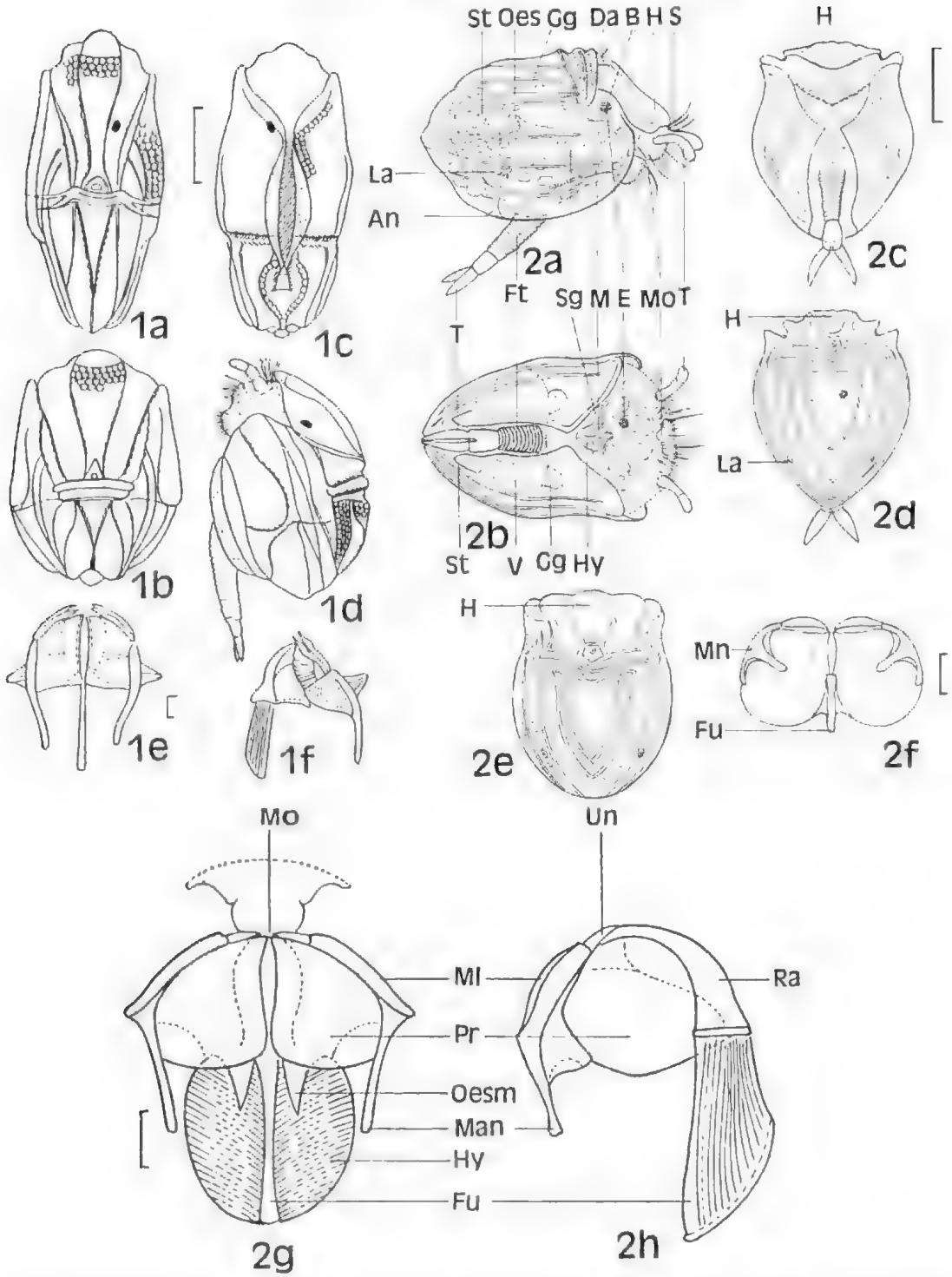


Fig. 4, 1. *Ploesoma lenticulare* Herrick: (a) dorsal; (b) dorsal, robust form; (c) ventral; (d) lateral, swimming; (e) trophus; (f) trophus, lateral. 2, *P. truncata* (Levander): (a) lateral; (b) ventral; (c) ventral, foot extended; (d) dorsal; (e) dorsal, contracted; (f) trophus, ventral; (g) trophus, dorsal; (h) trophus, lateral (B= brain; Da= dorsal antenna; E= eye; Ft= foot; Fu= fulcrum; Gg= gastric gland; H= headshield; Hy= hypopharynx muscle; La= lateral antenna; M= mastax; Man/Mn= manubrium; Ml= manubrial lamella; Mo= mouth; Oes= oesophagus; Oesm= insertion of oesophagus; Ra= ramus; SG= salivary gland; St= stomach; T= toe; V= vitellarium. (1 after Wulfert (1961), 2 after Koste (1982). Scale bars: adults 50 μm, trophi 10 μm.

BL 150-320 μm; FT 70 μm; T 18 μm; TR to 120 μm (FU 56 μm, M 34 μm, U 22 μm); RE 147×125 μm. A smaller morph from the Amazon (135 μm) has larger foot (79 μm) and trophi (128 μm: FU 77, R 51, M 23, U 26 μm) (Koste 1978a).

Distribution: Early record from N.S.W. (Whitelegge, 1889). Not seen again until Sept. 1991, when individuals of the robust morph (Fig. 4:1b) were found in samples from McCartney's Creek and Horseshoe Billabong in Barmah Forest (Vic.), persisting in the plankton until 12 Nov.: 15.0-21.2 °C, pH 7.3-7.6, 47-70 μS cm^{-1}.

Ploesoma truncata (Levander)
FIG. 4:2

Gastroschiza truncata Levander, 1894, p. 25, Fig. 1:9-10.
Ploesoma truncatum: Weber, 1898, p. 740, 743, Fig. 24: 8-10.

Type locality: Vicinity of Helsingfors (=Helsinki, Finland).

Description: Occipital margin almost straight, with lateral indentations; lines and furrows on dorsum form characteristic triangular ornamentation (Fig. 4:2d, e); foot partially annulated; toe of medium length; male unknown; RE with dark brown-black short-spined outer shell. Trophi: fulcrum rodlike in anterior view (Fig. 4:2g), broad, spatulate in lateral view (Fig. 4:2h); manubria crooked, almost 90° bend, both arms similar length, distal arm reaches only midpoint of fulcrum; large hypopharynx muscle for pumping.

BL 130-300 μm; FT 80 μm; TR: FU 36μm, M 26 μm either side of 'elbow', U 8 μm; SE & RE 60-70 ×82-90 μm.

Distribution: Single record from L. Ashwood, an acid dune lake near Strahan, W. Tasmania (Koste *et al.* 1988). 16.0 °C, pH 4.1, 131 μS cm^{-1}.

Polyarthra Ehrenberg

Polyarthra Ehrenberg, 1834, p. 226.

Body cylindrical, conical, saccate or cuboidal, in some species slightly flattened dorso-ventrally; cuticle transparent, stiffened; foot absent. At base of head, dorsal and ventral, two groups of three blade- or sword-shaped serrated finlike processes (variously termed finlets, fins, paddles or rudders) (Fig. 5) which are variable in length and width between populations. They are absent in first generation hatchlings from resting eggs. *P. dolichoptera* and *P. vulgaris* also have two obvious but shorter serrated fins on the ventral side (Fig. 6:1c). Corona of *Asplanchna* type; in apical field, two ciliated tentacles and sensillae; lateral antennae on distal third of body; trophi virgate (see Koste & Shiel 1987 for details of trophi structure); trophi musculature striated; vitellarium with 4, 8 or 12 nuclei; dwarf males are vasiform, finless, with ciliated penis and foot. Three form series were distinguished by Ruttner-Kolisko (1974), *viz: dolichoptera-vulgaris*, *remata-minor* and *major-euryptera*. At present, six of ten taxa listed in Koste (1978a) have been recorded from Australia.

Comment: The difficulty of specific determination from preserved contracted material was noted by Koste (1978a). He recommended calculation of indices of body:fin length and fin length:width, carmine staining of vitellaria, NaOCl-clearing for trophi analysis, etc. Comparative indices were used successfully by Guiset (1977) to separate *Polyarthra* species in Spanish reservoirs. Some intergrades of body and fin-lengths have been reported, so collection of all the relevant morphometric information for a particular population may not ensure specific placement. It is likely that trophi are species-specific, and will enable accurate species recognition.

Key to species of *Polyarthra* known from Australia

1. Ventral fins present (Fig. 6:1c) 2
   Ventral fins absent 3
2(1). FW >15 μm; trophi as Fig. 8:3b ..... *P. vulgaris* Carlin
   FW <15 μm; trophi as Fig 6:1b .... *P. dolichoptera* Idelson
3(1). BL >120 μm; vitellarium with 8 nuclei; trophi as Fig. 6:2b or 6:3b 4
   BL <120 μm; vitellarium with 4 nuclei; trophi as Fig. 8:1b or 8:2b 5
4(3). FW 8-11 μm; trophi as Fig. 6:2b ..... *P. longiremis* Carlin
   FW 20-37 μm; trophi as Fig. 6:3b ..... *P. major* Burckhardt
5(4). BL <70 μm; FW <5 μm; left dorsal fins notably longer than others; trophi as Fig. 8:1b ..... *P. minor* Voigt
   BL >80 μm; FW >5 μm; all fins similar length; trophi as Fig. 8:2b ..... *P. remata* (Skorikov)

Polyarthra dolichoptera Idelson
FIGS 5, 6:1

Polyarthra dolichoptera Idelson, 1925, p. 84.

Type locality: Novaja Zemla, Russia.

Description: Body an elongated cube, more slender

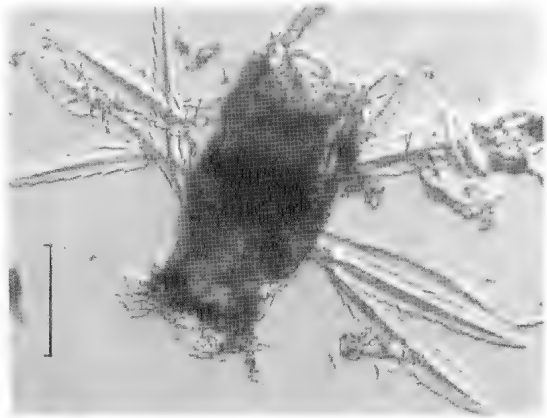


Fig. 5. *Polyarthra dolichoptera*, L. Hume, N.S.W. Dried onto slide to show fin morphology. Sony CVP-G700 video print. Scale bar = 50 μm.

than *P. vulgaris*; fins long, slender, extend beyond posterior margin; ventral fins fine, bristle-like, occasionally only a little broadened, finely serrated; median rib of fins distinct, continues to apex (Fig. 5) lateral ribs may be indistinct or absent; margins strongly serrated; lateral antennae at posterior corners; median eye; male known; RE with spinulate inner shell and rodlet reinforcement between inner and outer shells. TR asymmetric; each ramus resembles a hatchet with a single tooth on the 'blade' fitting a niche on the opposing blade; a reverse barb on distal end of blade leads to long, slightly convex 'handle' (bulla of ramus); viewed ventrally, lamellar rami form hemisphere (Fig. 6:1b); long rodlike fulcrum, broader in lateral view.

BL 90-140 μm; FL 110-220 μm; FW 7-15 μm; ventral FL 60-72 μm; TR 60 μm; SE with large oil droplets; RE 56-72×36-56 μm; index FL:BL >1.

Distribution: Pancontinental in billabongs or lakes, also in spring in lower R. Murray plankton, S.A. (Shiel *et al.* 1982). More common/abundant in cooler waters, with isolated occurrences above 15°C. 7.0-20°C, pH 4.8-8.2. DO 6.6-12.5 mg l^{-1}, 9-1650 μS cm^{-1}, 1.5-120 NTU.

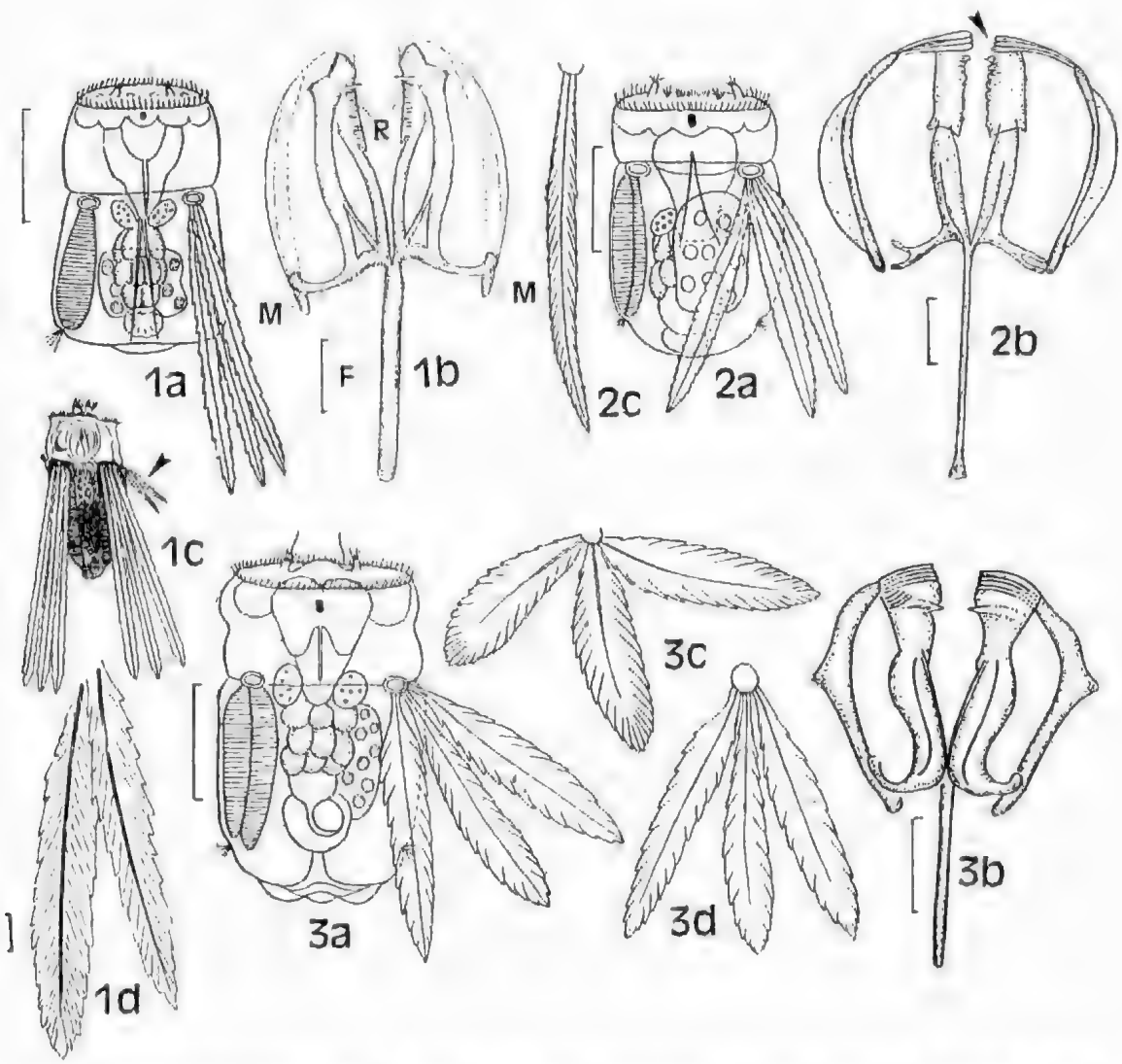


Fig. 6. 1. *Polyarthra dolichoptera* Idelson (a) lateral, only 1 set of fins shown, (b) trophus, dorsal (f = fulcrum, l = lamella in front of m = manubrium, r = ramus); (c) lateral with both lateral fin groups and shorter ventral finlets (arrowed); (d) fin morphology, l = Hume specimen from Fig. 5. 2. *P. longiremis* Carlin: (a) lateral, only 1 set of fins shown, (b) trophus, dorsal. (c) fin morphology: 3. *P. major* Burckhardt: (a) lateral, only 1 set of fins shown, (b) trophus, (c,d) fin groups, dorsal. (a, c, 2a, c, 3a, c, d after Kutikova (1962); 2b after Kutikova (1970). Scale bars: adults 50 μm, trophi 10 μm.

Polyarthra longiremis Carlin
FIG. 6:2

Polyarthra longiremis Carlin, 1943, p. 88, Fig. 1:3.

Type locality: Motala River, Sweden.
Description: Of similar body form to *P. vulgaris*, with wider caudal region; fins thin, commonly longer than body, reach considerably past posterior end; ventral appendages bristle-like. Vitellarium with eight nuclei; lateral antennae in distal ⅓ of body. TR symmetric, superficially similar to that of *P. dolichoptera* in ramus structure, but readily distinguished by three apical unci teeth opposing proximal to rami (arrowed in Fig. 6:2b), with serrate margins distal to unci; manubria curving rods with crescentic alulae on outer margin, meet subramal fossa at proximal end of fulcrum, almost at right angles to fulcrum (Fig. 6:2b).

BL 115-225 μm; FL 135-208 μm; FW 8-11 μm; ventral FL 61-66 μm; FL:BL >1; FL:FW>5.
Distribution: Recorded from Qld (Russell 1961), but not seen again until a 1985 sample series in Tasmania (Koste & Shiel 1986), where it occurred in Hydro-Electric Commission impoundments. It was found subsequently in a 1990 sample collected from L. Otaro, N.Z. (Coll. M.R. James, Taupo). 13.2-19.0°C, pH 4.2-6.8, 21-215 μS cm^{-1}.

Comments: P. longiremis probably is more widely distributed in Australasia than sparse records indicate. Close examination of trophi structure is vital for any *P. dolichoptera*-like rotifer collected at >15°C.

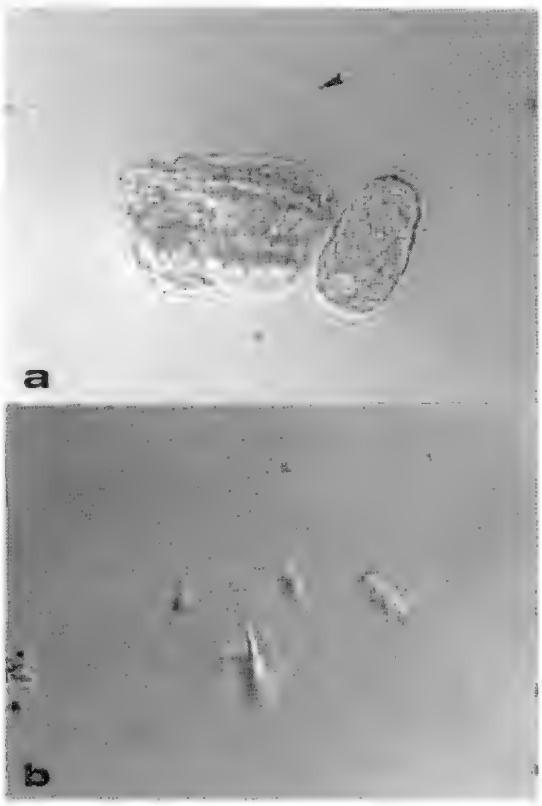


Fig. 7. *Polyarthra minor* Voigt: a, lateral, elongate dorsal fin set arrowed. BL 72 μm, egg 53×29 μm. b, trophus, 28 μm. Sony CVP-G700 video prints.

Polyarthra major Burckhardt
FIG. 6:3

Polyarthra major Burckhardt, 1900, p. 414.

Type locality: (Switzerland).
Description: Fins shorter than body, leaflike with midrib, feathered, weakly serrate; no ventral fins; lateral antennae inserted well before end of body; vitellarium with eight nuclei; male unknown; RE with outer colourless smooth shell and inner dark brown smooth shell. TR asymmetric: opposing rami teeth similar to those of *P. dolichoptera*. However, whereas ramus proximal to each tooth appears knoblike in dorsal view in *P. dolichoptera*, proximal ramus in *P. major* is serrated (cf. Fig. 6:3b); manubria with distinct 'elbow', ca. 120°.

BL 126-197 μm; FL 102-188 μm; FW 20-37 μm; FL:FW >5; FL:BL ≤1; RE 80-100×60-72 μm.
Distribution: Only two localities, Coliban Res and L. Catani, Vic., (Berzins 1982). Not seen in our material, unverified.

Polyarthra minor Voigt
FIGS 7, 8:1

Polyarthra minor Voigt, 1904, p. 33.

Type locality: Vicinity of Plön, Germany.
Description: Body relatively small and broad; lateral antennae medial; fins very slender; fins of left dorsal fin bundle considerably longer than other fins; vitellarium with four nuclei; SE carried attached; RE and ME unknown. Trophi asymmetric, similar to those of *P. remata*, although smaller; single pair of proximal large rami teeth, with series of smaller teeth distally (6-8), all fitting complementary niches in opposing ramus (Figs 7b, 8:1b); fulcrum rodlike in front view, with broader head laterally, i.e. similar shape to axe-handle.

BL 68-70 μm; FL 57-70/86-90 μm; FW 4 μm; FL:FW >5; FL:BL >1; TR 25-28 μm.

Distribution: Only known from a single locality, a billabong on Magela Ck floodplain, N.T. (Koste 1981, Tait *et al.* 1984), until 02.iii.92, when a population was recorded in Ryan's #2 Billabong on the R. Murray floodplain near Wodonga, Vic. 26°C, pH 7.7, 296 μS cm^{-1}. Probably more widely distributed.

Polyarthra remata (Skorikov)
FIG. 8:2

P. platyptera var. *remata* Skorikov, 1896, p. 71, Fig. 7:3-4.
Polyarthra remata: Rodewald 1938, p. 147.

Type locality: Vicinity of Kharkov, Ukraine.

Description: Fins longer than body; posterior rounded/lobed; lateral antennae just before posterior corner; eyespot dark red-black; fins slender with robust midrib, no laterals; vitellarium with four nuclei; RE with smooth outer shell and wrinkled inner shell. TR asymmetric: single pair of acute unci teeth oppose at proximal margin of rami in dorsal view (Fig. 8:2b, arrowed); inner rami margins with single large and several smaller teeth (Fig. 6:2c); external margins of rami curved, lamellate, similar to *P. dolichoptera*; manubria rodlike, curved, extend slightly beyond rami lamellae margin.

BL 80-120 μm; FL 80-110 μm; FW 7-8 μm; RE 48-60×32-44; FL:FW >5; FL:BL=1.

Distribution: Known only from Vic. (Berzins 1963) and Tas. (Koste & Shiel 1987b). 13-16°C.

Polyartha vulgaris Carlin
FIG. 8:3

Polyarthra vulgaris Carlin, 1943, p. 87, Fig. 13.

Type locality: Motala R., Sweden.

Description: Fins lanceolate, with medial and lateral ribs, margins serrate; fins may extend past body margin; ventral fins slightly broadened, lightly serrated; RE reddish-brown with smooth outer shell, hooked inner shell and intermediate folded membrane;

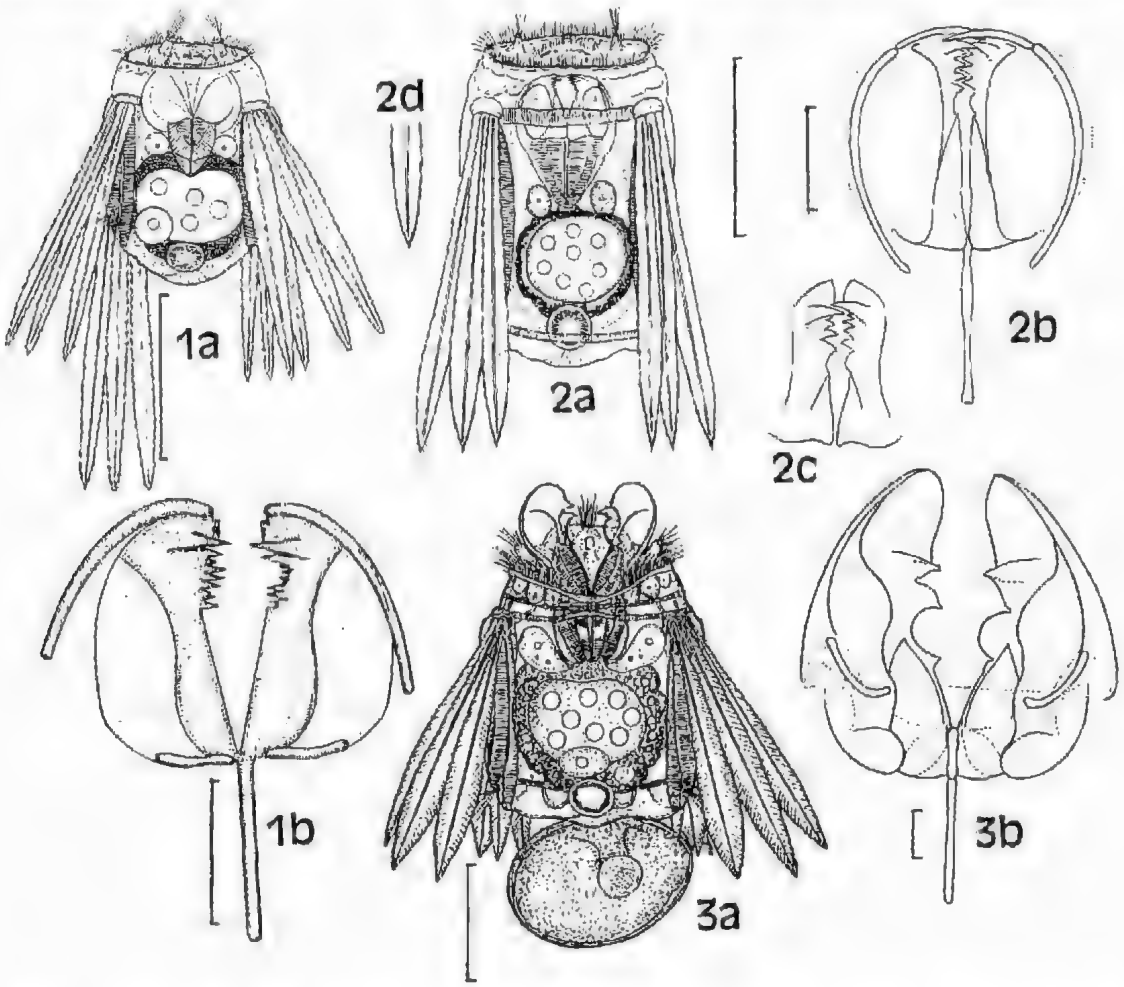


Fig. 8: 1, *Polyarthra minor* Voigt: (a) lateral; (b) trophus, dorsal; 2, *P. remata* (Skorikov): (a) lateral; (b) trophus, ventral; (c) rami dentition; (d) tip of fin. 3, *P. vulgaris Carlin*: (a) lateral, trophus extruded, and carrying parthenogenetic egg; (b) trophus, ventral (from Magela Creek, N.T. specimen) 1a, 2, 3b after Chengalath & Koste (1988). Scale bars: adults 50 μm, trophi 10 μm.

SE lightly coloured to transparent, with a large oil droplet; ME (up to six) carried attached; TR asymmetric; in dorsal view two large teeth on left ramus (Fig. 8:3b); single tooth on right ramus fits between them; rami borders distal to teeth hemispherical, complementary, left convex, right concave in dorsal view.

BL 100-145 µm; FL 118-160 µm; FW 16-20 µm; ventral Fl. 30-70 µm; RE 78-88×52-60 µm; SE 76×50 µm; ME 26×26 µm.

Distribution: Most common *Polyarthra* in Australian waters, pancontinental in lentic waters, also common in lower R. Murray plankton (autumn) (Shiel *et al.* 1982). 7.2-29.0°C, pH 4.9-8.7, DO 1.5-12.0 mg l^{-1}, 13-1100 µS cm^{-1}, <1-110 NTU.

Synchaeta Ehrenberg

Synchaeta Ehrenberg, 1832, p. 135.

Cuticle transparent, pliable; body conical-vasiform, depending on ingested food, size of vitellarium and egg development; foot short, one-segmented; toes generally acute; corona an interrupted circumapical band with widely projecting ciliary auricles; apical field with four styli, elongated ciliated tentacles and sensillae; dorsal antenna in neck; lateral antennae in posterior ⅓ or at base of foot; mastax large with distinct striated muscles; trophi virgate, large, delicate; fulcrum and manubria long, thin; in some taxa unci acute, with comblike serrated edge; internal organ is as in Fig. 8:1. SE and RE appear to have species specific morphology; males are known for some species only; >30 species described globally, but taxonomic resolution imprecise. About 20 of these are from athallasic saline or marine waters (Ruttner-Kolisko 1974; Koste 1978a). Marine rotifers, including synchaetids, have been neglected in Australasia. Only *S. baltica* has been reported off Port Jackson by Whitelegge (1889), and in Port Phillip Bay (Evans 1951). It is not included in the key, but a description is given for convenience. It is likely that further marine species of *Synchaeta*, *inter alia*, will be found here. A list of known marine synchaetids and relevant bibliography is given by Ruttner-Kolisko (1974). Ten *Synchaeta* species have been reported from inland waters, including a new endemic species described here. It was first recorded by the late C. R. Russell, Christchurch N.Z., from a sample taken in 1959 in Warragamba Dam but apparently not described.

Key to species of Synchaeta known from Australia

1. Uncus of trophus with one main tooth, no accessory teeth 6
   Uncus with main and accessory teeth 2
2(1). Lateral antennae in posterior third of body 3
   Lateral antennae near base of foot ..... *S. tremula* (Müller)
3(2). Marked constriction below ciliary auricles (Fig. 8:3a) ..... *S. lakowitziana* Lucks
   No obvious constriction 4
4(3). Body cylindrical; auricles small; toes 9-10 µm; unci with 4-5 robust teeth ..... *S. tavina* Hood
   Body coniform; auricles not small; toes ≤5 µm; unci with 5-8 teeth 5
5(4). Apical field flat; uncus 6-8 toothed ..... *S. oblonga* Ehrenberg
   Apical field domed; uncus 5-6 toothed ..... *S. littoralis* Rousselet
6(1). Two large ciliated tentacles in apical field ..... *S. pectinata* Ehrenberg
   Apical field smooth or with ciliated humps 7
7(6). Trunk medially constricted, elongated (Fig. 8:2a); BL >400 µm ..... *S. grandis* Zacharias
   No obvious constriction, trunk convex at sides; BL to 320 µm 8
8(7). BL <200 µm; foot elongated 9
   BL 200-313 µm; foot not elongated ..... *S. stylata* Wierzejski
9(8). BL >150 µm; foot and toes as Fig. 12:3 ..... *S. longipes* Gosse
   BL <150 µm; foot and toes as Fig. 11:1 ..... *S. jollyi* sp.nov.

Synchaeta baltica Ehrenberg
FIG. 9:1

Synchaeta baltica Ehrenberg, 1834, p. 220.

Type locality: (?Europe).

Description: Bell-shaped/conical; foot long, cylindrical; trunk may be annulated in posterior; toes short; foot glands short, indistinctly separated; lateral apical sensillae on papillae; male not described; RE with projecting integument. TR not described.

BL 190-523 µm.

Distribution: Marine, estuarine, coastal waters worldwide. Two records: one off Sydney (Whitelegge 1889) and Port Philip Bay (Evans 1951).

Synchaeta grandis Zacharias
FIG. 9:2

Synchaeta grandis Zacharias, 1893, p. 23, Fig. 2.

Type locality: Plöner See, Germany.

Description: Body very long, usually cylindrical behind medial constriction; colourless except for yellowish tint to ciliary auricles and protruding apical field; foot and foot glands long; toes very short; eye red or black, circular; oesophagus very long. Trophi: uncus a broad plate with very fine denticles (Fig. 9:2c); fulcrum long, slender; manubria with semicircular outer lamellae; male undescribed; SE, RE, ME with fine spines.

BL 400-600 µm; head width 180-200 µm; SE & RE 80-92×70-80 µm; ME 56×54 µm.

Distribution: Rare in our samples (5 of ca. 5000 to date): billabongs & mainstream R. Murray near Wodonga, Vic., Yarnup Swamp, W.A. and a single record of a *Synchaeta* resembling *S. grandis* from a humic stock dam at Karanja, near Mt Field National

Park, in Tasmania (28.IX.87) (Koste *et al.* 1988): 10-16°C, pH 6.0-7.6, DO 10.7 mg l^{-1}, 64-166 μS cm^{-1}, 8 NTU.

Synchaeta sp. nov.

While a Visiting Researcher at Waikato University in May-June 1993, RJS chanced upon the notes of the late C. R. Russell held at the Canterbury Museum in Christchurch, N.Z. Cecil Russell was the "Honorary Keeper of Rotifers" at the Museum until his death in 1961, and had published extensively on the N.Z. rotifers in the period 1945-1961, with two papers including Australian rotifers (Russell 1957, 1961). In one of his laboratory notebooks, he listed "*Synchaeta* n. sp." from a sample collected in Warragamba Dam, N.S.W., by V. H. Jolly, (W2 27.X.59). The brief description and pencil sketches of animal and trophi in Russell's laboratory notebook (Fig. 11:1a, b) were not published prior to his death, and the taxon had not been collected again. We could not recognise it as one of the known *Synchaeta* species reviewed by Koste (1978). Fig. 11:1a, b are copied from ca. p. 49 of Russell's "Feb. 1 1960 – Australian Rotifers" notebook, and the description below from the following page. The text is verbatim, parentheses are used where a word is not clear, and some punctuation has been inserted

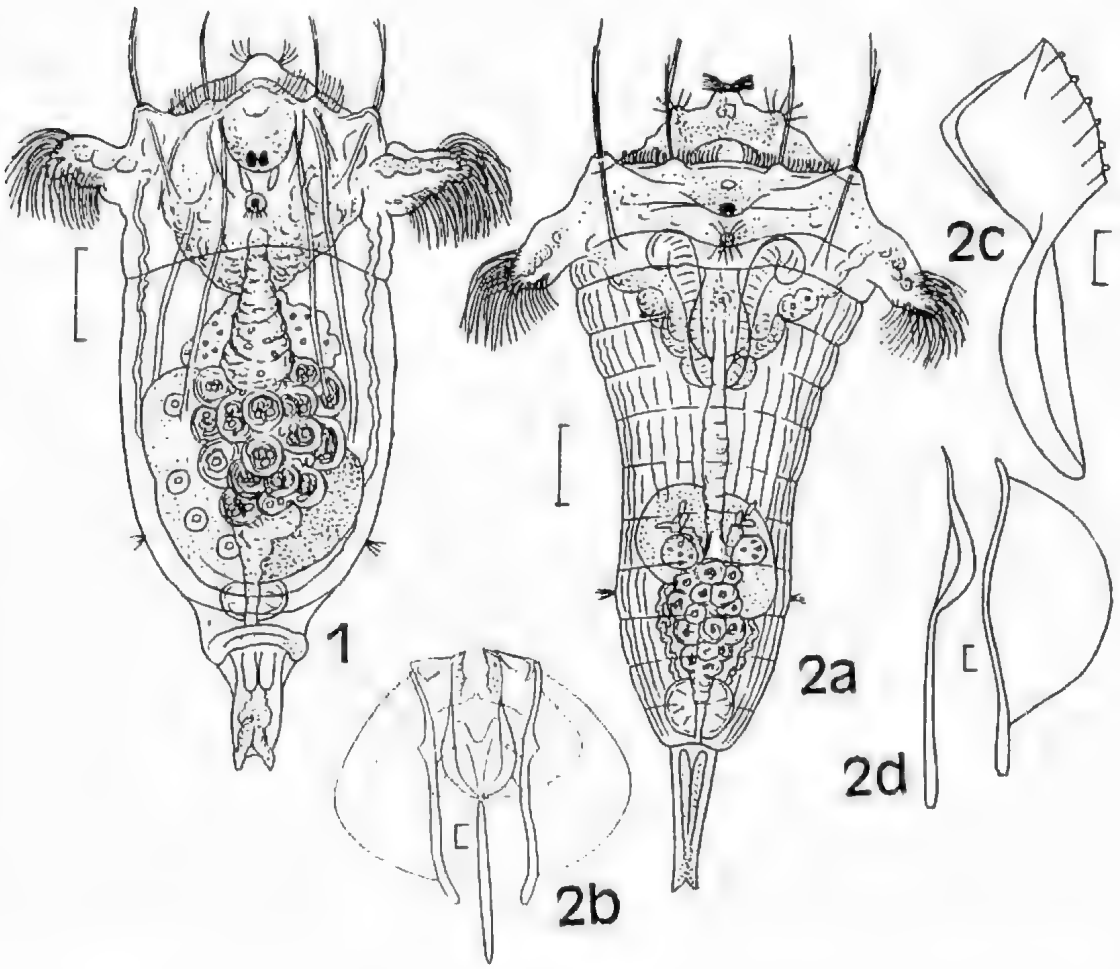


Fig. 9, 1, *Synchaeta baltica* Ehrenberg, dorsal. 2, *S. grandis* Zacharias: (a) dorsal; (b) uncus and ramus; (c) ramus and fulcrum; (d) manubrium, two views. 1, 2a after Rousselet (1902); 2b after Stemberger (1979); 2c, d after Kutikova (1970).. Scale bars: adults 50 μm, trophi 10 μm

"*Synchaeta* n.sp.
Body conical, small; auricles small with weak cilia. Foot obsolete, toe single, with enigmatic dirty end, (immovable); antennae 4 short. Trophi with single tooth on each ramus, a modification of *pectinata* type having one tooth in each ramus; the rami are slightly triangular.
Length of body 120-130 μm. Length of toe 10 μm. Length of trophi 70-80 μm.
In the contracted animal has a marked curved anterior margin. This animal differs from other species of *Synchaeta* in its small size (*these two words have been crossed out*) (unmistakable) toe, absence of foot, difference in trophi, particularly the plate."

No material could be found in the Russell slide collection held at the Canterbury Museum. To determine the identity of this taxon, the assistance of Tsuyoshi Kobayashi at Australian Water Technologies, Science and Environment was sought. He found early collections (Nov. 1965) by Sydney Water Board from Warragamba Dam which contained four individuals of a *Synchaeta*, but Russell's species was not present. The species was therefore described as *Incertae sedis* in the first draft of this paper. Fortuitously, Fitzroy R. samples sent by Larelle Fabbro, from the University of Central Qld, arrived while the MS was with referees. The first specimens encountered (by RJS) were undoubtedly the same as those seen by Russell. Several were sent to WK, who verified that the taxon, although similar to *S. longipes*, appeared to be new.

Synchaeta jollyi sp.nov.
FIGS 10-12

Type locality: impoundment of Fitzroy R., near Ramsey Ck inlet, 70 km upstream of barrage at Rockhampton Qld, (approx. 23°05'S/150°00'E), 07.i.1993, Coll. L. Fabbro, Univ. Central Qld, Rockhampton.
Holotype: Single female, mounted in glycerine-gelatine. South Australian Museum (SAM) V4244. Date and place of collection as above.
Paratypes: Four females on slide V4245, SAM. Date and place of collection as above. Two slides, *Synchaeta* collection, MDFRC #4090. 30 ml plankton sample containing *S. jollyi* from Fitzroy R., Qld, MDFRC #4090. Date and place of collection as above.
Material examined: Ten females were examined and measured.
Description: (from partially contracted individual). Small conical body; head slightly convex; auricles small, face forward, with slight lateral bulges in slightly contracted animal; body broad for two-thirds of length, tapers to rounded posterior (Fig. 10, 11;2a); single median crimson cerebral eye; lateral antennae at midline; distinctive long cylindrical foot, not retracted in preserved individuals, presumably not retractible. *S. longipes* has an elongated retractible foot; paired foot glands elongated, cylindrical; two minute toes, barely discernible. Trophi: large in relation to body; uncus single toothed (Fig. 12a) (cf. *S. pectinata*); fulcrum straight, rodlike in anterior view, slightly curved in lateral view (Fig. 12b); manubria curved with hemispherical lamellae; male unknown; SE, RE, ME unknown. BL 107±7.8 μm; BW 90±4.2 μm; F/T 23.6±4.5 μm; TR 70-82 μm (FU 54 μm, M 68 μm).
Distribution: Only two localities known: type locality, the Fitzroy R. near Rockhampton, Qld., and Warragamba Dam (now L. Burragorang) N.S.W., one of Sydney's water-supply reservoirs. Probably more widespread.
Etymology: This rotifer is named after the late Dr Violet Hilary Jolly, one of Australasia's first fresh-water ecologists. While with the Sydney Water Board in 1959, she collected the samples which ultimately led to the rediscovery of this species.

Synchaeta lakowitziana Lucks
FIG. 13:1

Synchaeta lakowitziana Lucks, 1930, p. 59, Figs A-F.

Type locality: (?Europe).
Description: Marked constriction in neck region noted in original description possibly artefact of cocaine narcotization and formalin preservation; plump elongate body; dorsally, shape of head pentagonal; lateral sensillae on short papillae; toes acute; vitellarium bilobed; foot glands small. Trophi: unci plates with 1-2 large dagger-like teeth and 6-7 accessory teeth (Fig. 13:1c); SE smooth, RE spinulate.

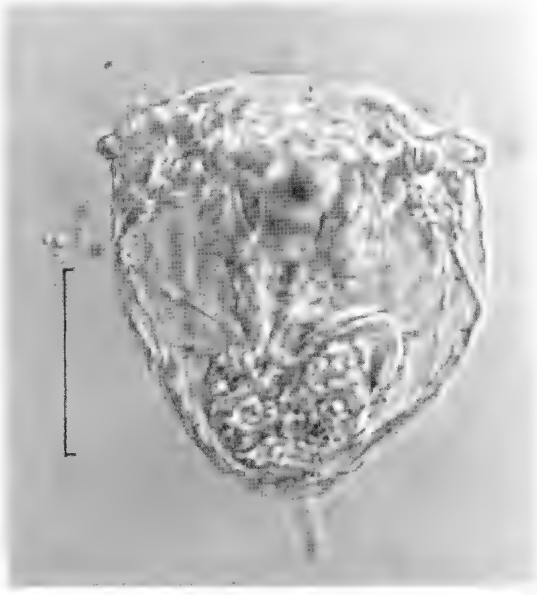


Fig. 10: *Synchaeta jollyi*, sp.nov. Fitzroy R., Qld. Coll. L. Fabbro, Univ. Central Qld. Sony CVP-G700 video print. Scale bar = 50 μm.

TL 350-300 μm; male 110 μm; RE 72×64 (Fig. 13:1f) or 67×45 μm with 15 μm long spines (Fig. 13:1g).

Distribution: In Europe, cold stenotherm in winter plankton of mountain lake hypolimnia and arctic waters. Three Australian localities known, but in view of European habitat preferences of this species, all populations require detailed examination: two mainland rivers: Moorabool R., Vic. in 1954 (Berzins 1982), lower R. Murray in S.A. (Shiel & Koste 1985), and a humic roadside pool near L. Garcia in W. Tasmania (Koste *et al.* 1988), 17.0-17.5°C, pH 3.1-7.0, 81-500 μS cm^{-1}, <1-150 NTU.

Synchaeta littoralis Rousselet
FIG. 13:2

Synchaeta littoralis Rousselet, 1902, p. 398, Fig. 7:15.

Type locality: (U.K.).

Description: Resembles *S. oblonga*, but apical field more domed; two-part cerebral eyspot with stream of

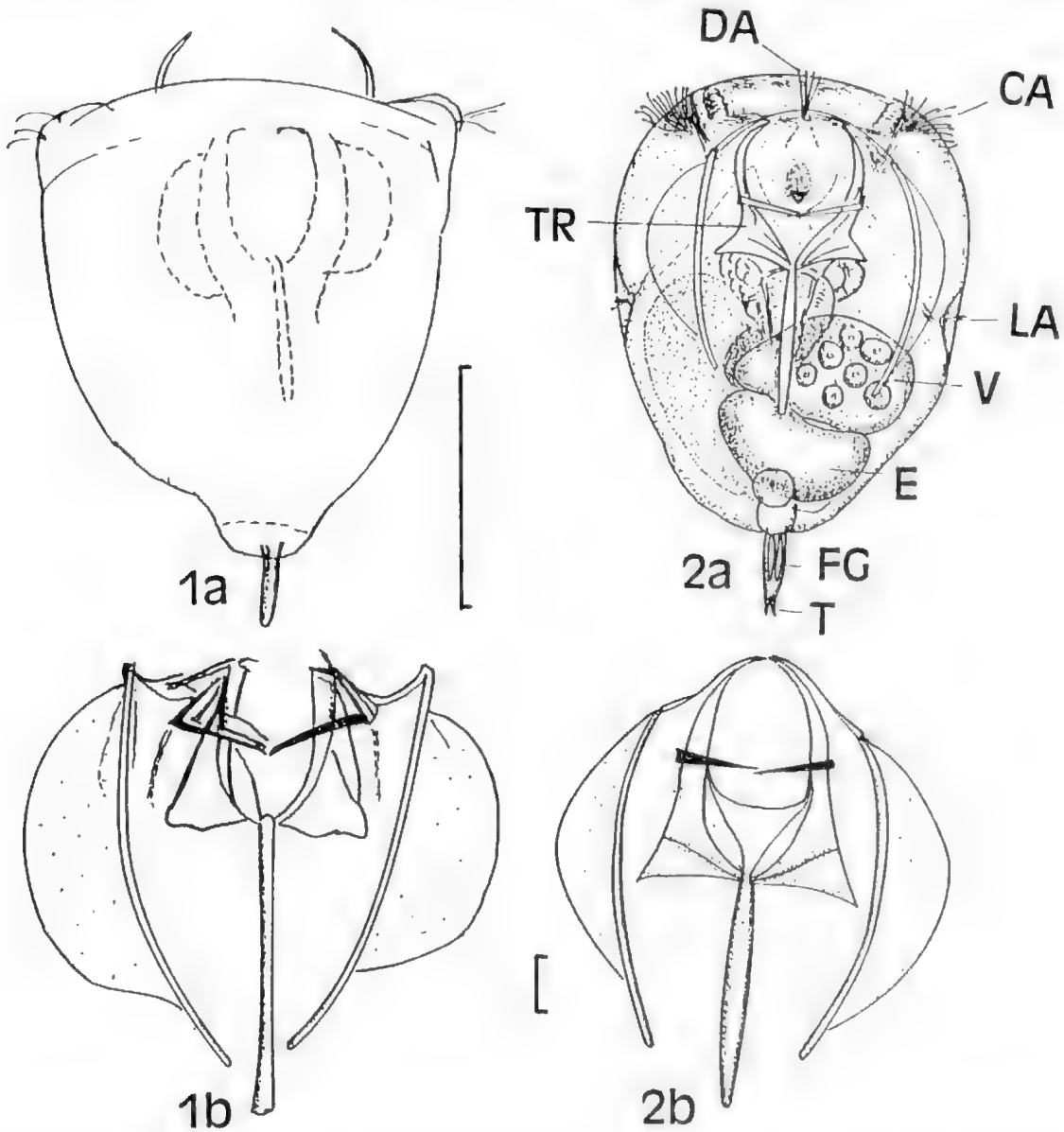


Fig. 11. *Synchaeta jollyi*, sp.nov. 1, (a) contracted; (b) trophus. 2, (a) contracted, (b) trophus. 1 from original pencil sketch by C.R. Russell, Canterbury Museum, Christchurch, N.Z. Coll. Warragamba Dam, 27.X.59, V.H. Jolly. 2, Fitzroy R. specimen. Scale bars: adults 50 μm, trophi 10 μm.

red granules to large red cervical eyespot; pigment granules diffuse in cold period, increase in density in spring; foot trapezoid; toes very short. TR undescribed.

TL 192-290 μm; toe 5 μm.

Distribution: *S.* cf. *littoralis* was collected in a billabong at Wodonga, Vic. (winter) (Koste & Shiel 1980), 10.2°C, pH 7.2, DO 9.0 mg l^{-1}, 154 μS cm^{-1}, 4 NTU. A few individuals were collected in L. Colongulac, Vic. (17.V.80), 13.0°C, no other ecological information.

Synchaeta longipes Gosse
FIG. 13:3

Synchaeta longipes Gosse, 1887, p. 5, Fig. 2:15.

Type locality: " . . . near Dundee". Lacustrine.

Description: Broad, protruding triangular head with widely spaced ciliary auricles directed somewhat posteriorly; body broadest at level of lateral antennae; foot clearly demarcated from body, cylindrical, long, thin, with two small toes; cuticle transparent or with bluish tinge; mastax orange-red, occasionally with bluish flecks in trophus region. Trophus: unci with acute robust tooth; manubria slightly sigmoidal with small triangular alulae on proximal third of external margin; SE rounded ellipsoid, smooth shelled; RE with rodlets between shells; yellow RE contents contain red-orange oil droplets; male unknown.

TL 164-204 μm; T 6-7 μm; SE 60×56 μm; RE 72-76×56-60 μm.

Distribution: Probably pancontinental, not yet recorded from W.A. Rare, in billabongs and rivers, in winter-spring plankton of lower R. Murray, S.A. (Shiel *et al.* 1982): 8.5-27.0°C, pH 6.2-8.5, DO 6.3-10.4, 27-400 μS cm^{-1}, <1-160 NTU.

Synchaeta oblonga Ehrenberg
FIG. 13:4

Synchaeta oblonga Ehrenberg, 1832, p. 135.

Type locality: (?Europe).

Description: Variable morphology; trunk generally barrel-shaped, laterally convex, but may be bell-shaped or ovoid; cuticle with longitudinal striae, colourless or yellowish; foot conical, toes short, bulbous; eyespots of different size, generally separated, also with speckled pigment granules; some populations may have fused eyespots; dorsal antenna normal; lateral antennae minute. TR: unci 6-8 toothed, generally symmetrical with notch behind main tooth and second notch behind

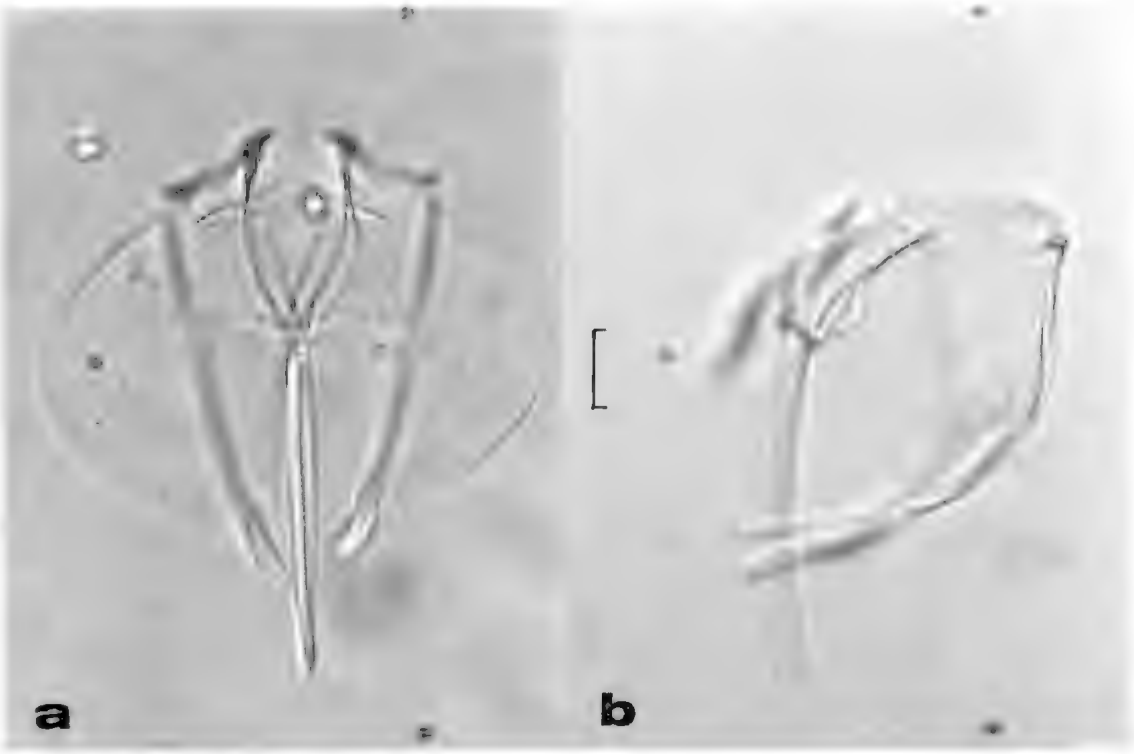


Fig. 12: *Synchaeta jollyi* sp.nov. Trophus (a) dorsal, (b) lateral. Sony CVP-G700 video prints. Scale bar = 10μm.

group of accessory teeth (Fig. 13:4c). Rami with rounded alulae; manubria with distal barlike flattening and semicircular alulae; SE carried only a short time; RE with short spines on inner and outer shell; male known.

TL 225-250 μm; male 95-102 μm; SE 62×58 μm; RE 56-64×56-60 μm.

Distribution: In reservoirs, billabongs and rivers, most common of the smaller *Synchaeta* species in our samples, often with *S. pectinata*. NSW, Tas., Vic., W.A. Probably more widely distributed in Australia than present limited records indicate. 9.0-23.0, pH 4.8-10.0, DO 6.2-11.0 mg l^{-1}, 9-1650 μS cm^{-1}, 2-150 NTU.

Synchaeta pectinata Ehrenberg
FIG. 13:5

Synchaeta pectinata Ehrenberg, 1832, p. 135.

Type locality: (?Europe).

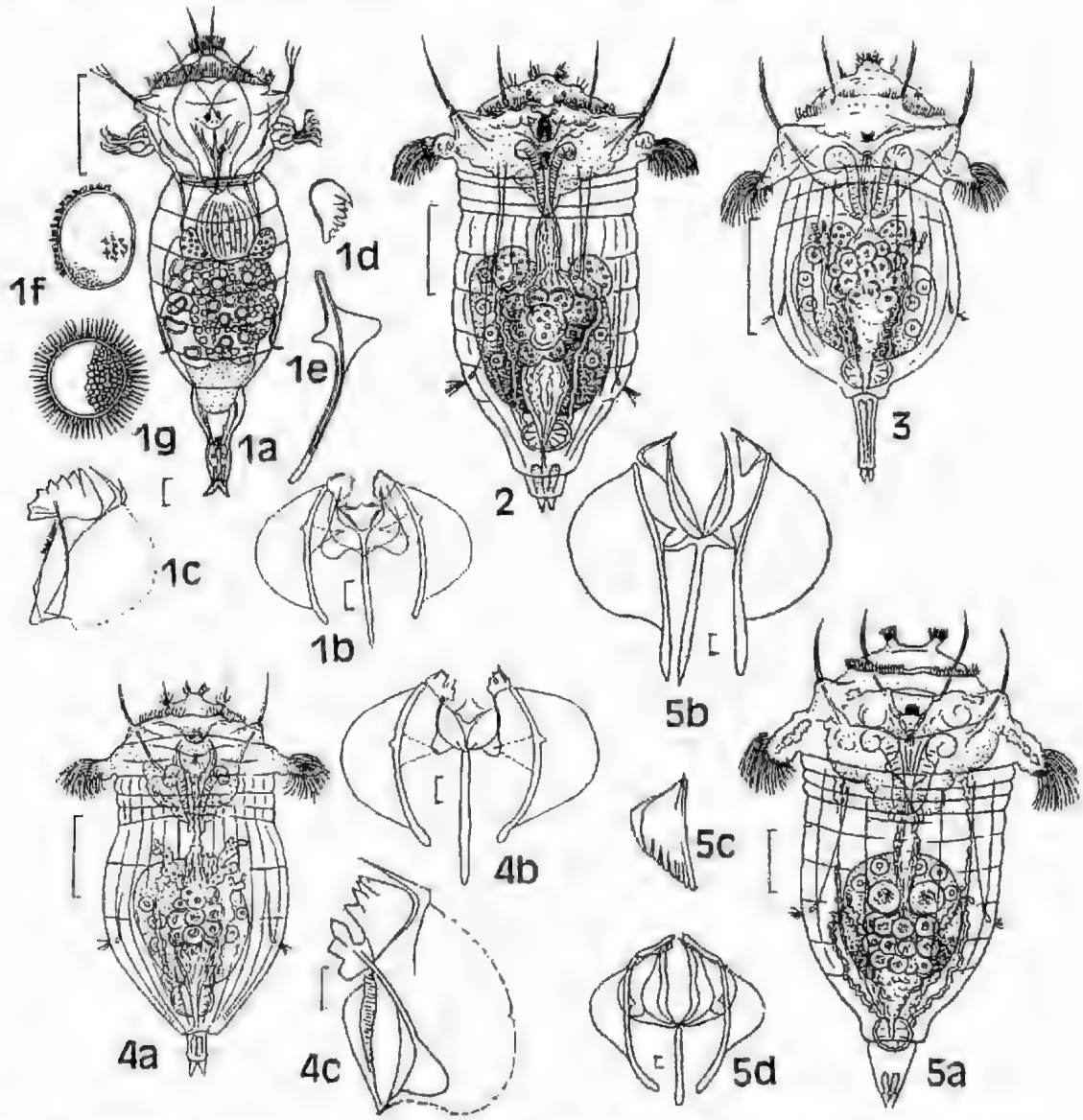
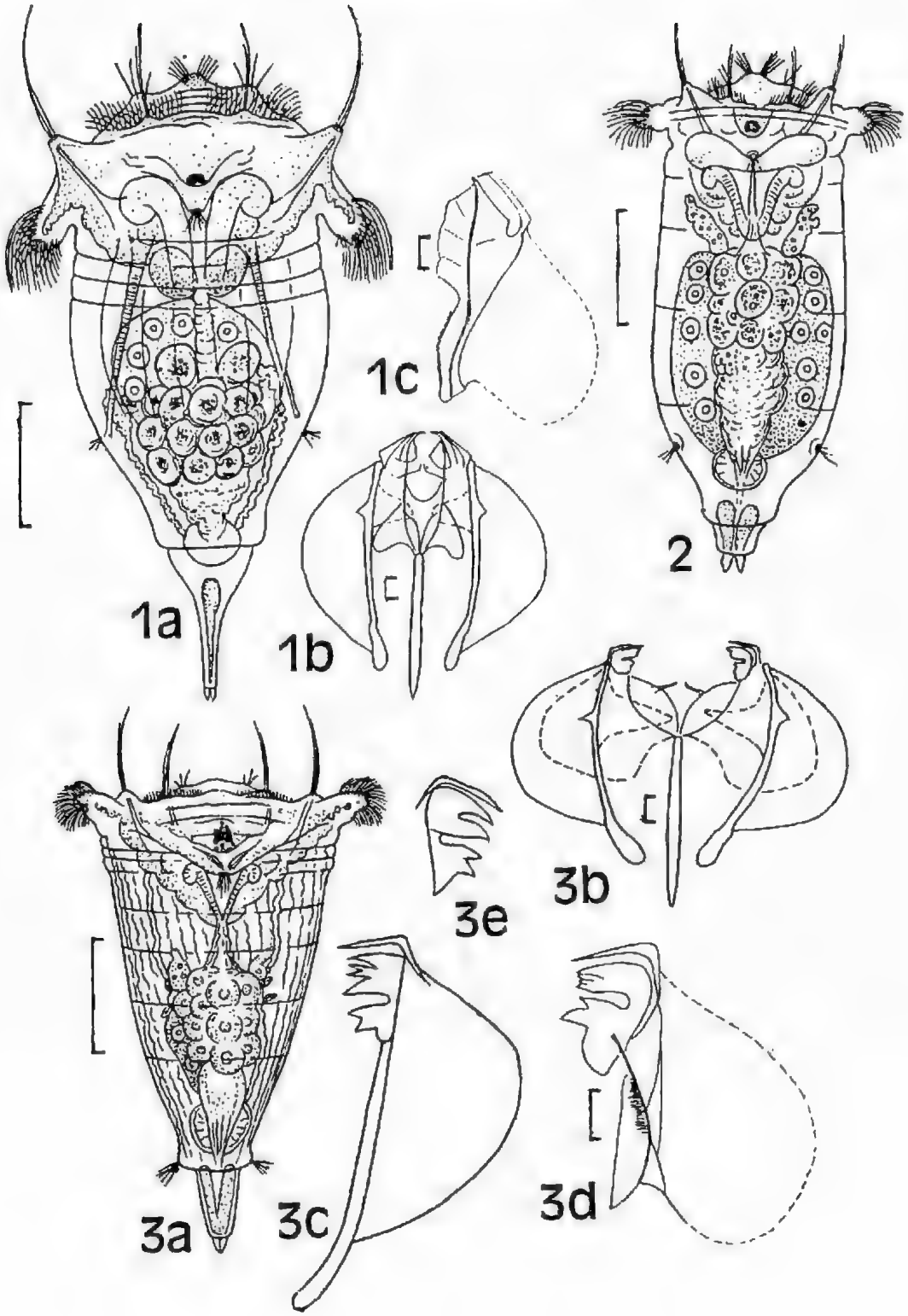


Fig. 13. 1, *Synchaeta lackowitziana* Lucks: (a) dorsal; (b) trophus; (c) uncus & ramus; (d) uncus; (e) manubrium; (f,g) resting eggs. 2, *S. litoralis* Rousselet: dorsal. 3, *S. longipes* Gosse: dorsal. 4, *S. oblonga* Ehrenberg: (a) dorsal; (b) trophus; (c) uncus & ramus. 5, *Synchaeta pectinata* Ehrenberg. (a) dorsal; (b,d) trophi; (c) uncus. 1a, d-g after Lucks (1930); 2, 3, 4a, 5a, d after Rousselet (1902); 1b, c, 4b, c after Stemberger (1979); 5c, d after Kutikova (1970). Scale bars: adults 50 μm, trophi 10 μm.


1a
1b
1c
2
3a
3b
3c
3d
3e

Description: Two ciliated tentacles in apical field; foot short and wide; toe relatively small; foot glands shorter than foot; eyespot dark red or purplish; lateral antennae at beginning of distal third of body. TR: uncl platelike with grooved facing margins; rami crescentic, acute at proximal tips; fulcrum long, rodlike viewed dorsally, broader laterally; manubria rodlike with median shallow U-bend; broad crescentic lamellae along ca. ¼ of outer manubrium (Fig. 13:5b, d); SE with oil droplets and gelatinous sheath; RE either thin-shelled with small hooks or more robust and spiny.

TL 240-550 μm; toes 5-8 μm; male 160 μm; TR 190 μm; SE 75 μm; RE 80-90 μm.

Distribution: Largest and most common *Synchaeta* in our samples; pancontinental in billabongs, stock dams, lakes and impoundments, also in lowland rivers; autumn-winter occurrence in lower R. Murray (Shiel *et al.* 1982). 7.0-29.0°C, pH 3.9-8.7, DO 4.0-10.6 mg l^{-1}, 9-1000 μS cm^{-1}, <1-150 NTU.

Synchaeta stylata Wierzejski
FIG. 14:1

Synchaeta stylata Wierzejski, 1893, p. 404

Type locality: Galicia, Poland.

Description: Resembles *S. longipes;* body tapers to base of foot; foot arises from a broader base than in other species, is not as clearly demarcated from trunk; toes very short; apical field mostly smooth, eyespot single, occasionally paired; lateral antennae in distal third of body; male known; SE and ME with relatively long, delicate bristles, RE with shorter bristles into gelatinous sheath; TR: uncl tips curve inwards; manubria lamellae margin serrated.

TL 200-313 μm; FT 33-50 μm; T 4 μm; Male 89 μm; SE 64-74×50 μm; RE 80×68 μm.

Distribution: Uncommon in NSW, Qld, but most common and perennial *Synchaeta* in lower R. Murray plankton, S.A. (Shiel *et al.* 1982). 8.0-27.0°C, pH 7.0-8.5, DO 7.0-11.8, 60-1100 μS cm^{-1}, 1-110 NTU.

Synchaeta tavina Hood
FIG. 14:2

Synchaeta tavina Hood, 1893, p. 382, Fig. 17.

Type locality: (?U.K.).

Description: Body almost cylindrical; auricles small; foot and toe short; vitellarium with 8-12 nuclei; foregut present; eyespots generally paired, occasionally single larger fused eyespot (may be violet-red); lateral antennae deeply inserted; TR: uncl with 4-5 robust teeth; rami with triangular upcurving alulae; fulcrum rodlike distally, laterally forms a striate semicircle

BL 176-254 μm; a 176 μm specimen was 61 μm wide at the head with T 9-10 μm; TR 56 μ FU 26 μm, R 38 μm, M 40 μm)

Distribution: Rare, recorded from only four localities, a flooded gravel pit nr Eildon, Vic., Cullen's L. and Little Coliban Res., Vic., single record in lower R. Murray plankton, S.A. (spring) (Shiel *et al.* 1982) 18.0-23.0°C, pH 7.0-8.0, DO 8.3-11.0 mg l^{-1}, 70-602 μS cm^{-1}, 65 NTU.

Synchaeta tremula (Müller)
FIG. 14:3

Vorticella tremula Müller, 1786, p. 280, Fig. 61.4-7.
Synchaeta tremula: Ehrenberg 1832, p. 135.

Type locality: (Europe).

Description: Barrel- to cup-shaped body, often yellowish in colour; cuticle with striae; toes short, stout; eyespots sometimes with clusters of pigment granules; transitional forms with *S. oblonga* are known, also seasonal variants and ?ecotypic morphs in brackish saline waters (Koste 1978a); SE smooth-shelled, occasionally in gelatinous sheath; two RE forms: with fine bristles or with short spines. Male known. TR: uncl asymmetric, each uncus with single main tooth, 4-6 accessory teeth, also smaller denticles, separated by deep notches. Manubria slightly thickened medially.

BL 150-328 μm; T 8-11 μm; Male 110 μm; SE 93×76 μm; ME 62×51 μm; RE 75×68 μm.

Distribution: Rare, eleven records from Barwon R., Qld and downstream Darling R., N.S.W., central Tasmania, Waranga Basin and upper Murray billabongs, Vic. 10.0-16.0°C, pH 4.9-9.2, DO 8.1-10.0 mg l^{-1}, 19-355 μS cm^{-1}, 4.0 NTU.

Family Asplanchnidae Harring & Myers, 1926

Relatively large animals (to 2.5 mm); cuticle thin, transparent, but retains shape, which may be saccate, pear- or barrel-shaped, sometimes with lateral protrusions (cf. Fig. 17:5a); foot and toes are present in the swimming or creeping *Harringia*, rudimentary in semiplanktonic *Asplanchnopus*, lost in *Asplanchna*, an adaptation to a fully pelagic existence. Corona of *Asplanchna*-type (see Koste & Shiel 1987). All three genera have incudate trophi, that of *Harringia* does not have a suction function. *Asplanchnopus* and *Asplanchna* do not have intestine, cloaca or anus. *Harringia* is not known from Australia. Two species of *Asplanchnopus* and seven of *Asplanchna* are known from Australia; one species, *A. asymmetrica*, is endemic.

Fig. 14. 1, *Synchaeta stylata* Wierzejski: (a) dorsal; (b) trophus, (c) uncus & ramus. 2, *S. tavina* Hood, dorsal. 3, *S. tremula* Ehrenberg: (a) dorsal; (b) trophus; (c) uncus, ramus & manubrium; (d) uncus & ramus, (e) uncus. 1a, 2, 3a, c after Rousselet (1902); 1b, c, 3b, d after Stemberger (1979); 3e after Kutikova (1970). Scale bars: adults 50 μm, trophi 10 μm

Key to genera

With rudimentary foot and toes, ... *Asplanchnopus* De Guerne
Foot and toes absent ..... *Asplanchna* Gosse.

Asplanchnopus De Guerne, 1888

De Guerne 1888, p. 57.

Cuticle flexible, transparent; body saccate or pear-shaped, with or without protrusions; corona divided circumapical ciliary band; apical field with bundles of sensillae; one cerebral eyespot and two lateral ocelli on short papillae in circumapical band; paired dorsal antennae; retrocerebral organ and subcerebral glands small; vitellarium spherical, riboon- or horseshoe-shaped, with eight or many nuclei; foot short or long, unsegmented, annulated or with a single distinct foot segment; toes conical, tiny or lamelliform; oviparous or viviparous.

Key to species of Asplanchnopus known from Australia

Dorsal antennae divided, widely separated; >50 pairs of protonephridial flame cells; trophi >100 µm ..... *A. multiceps* (Schrank)
Dorsal antennae partly fused; 8-13 flame cells; trophus <75 µm ..... *A. hyalinus* Harring

Asplanchnopus hyalinus Harring
FIG. 15:1

Asplanchnopus hyalinus Harring, 1913, p. 402, Fig. 32: 3-4

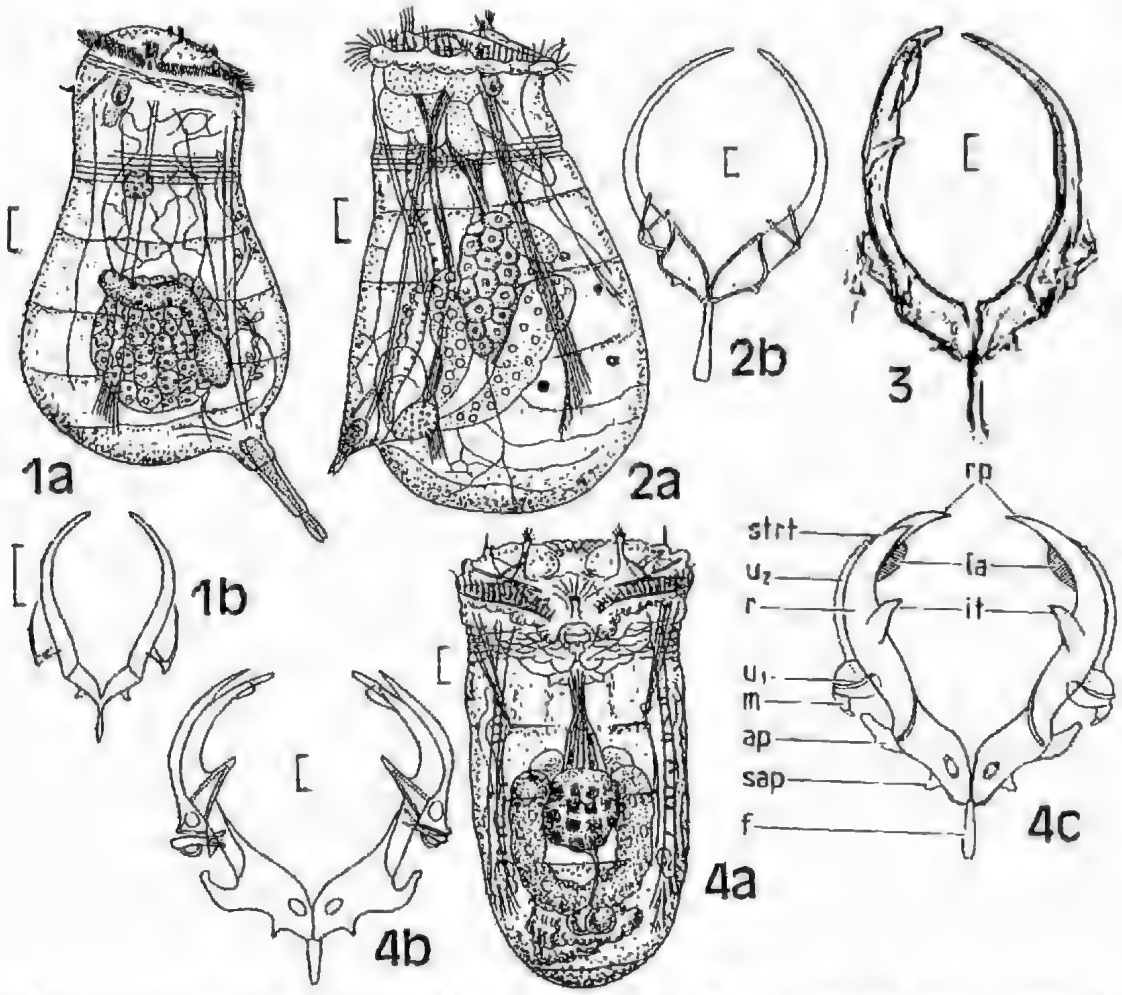


Fig. 15. 1, *Asplanchnopus hyalinus* Harring: (a) lateral; (b) trophus. 2, *A. multiceps* Schrank: (a) lateral; (b) trophus. 3, *Asplanchna asymmetrica* (Koste & Shiel), trophus. 4, *A. brightwelli* Gosse: (a) dorsal; (b) trophus; (c) trophus, diagrammatic (up= apophysis on bulla of ramus; f= fulcrum; it= inner teeth on rami inner margins; la= lamella behind rami points; m= manubrium; r= ramus; rp= rami apices; sap= subapophysis; strt= second ramus tooth; u_1= 1st uncus; u_2= 2nd uncus). 1 after Harring (1913), 2 after Weber (1898), 3, 4c after Shiel & Koste (1985), 4a after Hudson & Gosse (1886), 4b after Hauer (1952).

Type locality: Four-mile Run, near Washington, D.C., U.S.A.

Description: Body moderately elongate; slight constriction between head and trunk; foot about one-third body length, segmented, distal joint twice as long as proximal; toes lamelliform, similar length as first foot-joint; pedal glands as long as entire foot; corona with interrupted circumapical band, ventrally at mouth and laterally by two small papillae bearing ocelli; cerebral eye present; mastax large, trophi incudate, distinguished from other species in the family by lack of inner teeth or reinforcing ribs; short oesophagus, large stomach with pair of gastric glands opening into anterior region; eight pairs of protonephridial flame cells; ovary ribbon-shaped. ?Oviparous.

BL 520-660 μm; FT 90-120 μm; T 32-40 μm; TR 63-75 μm.

Distribution: Carnivore on small rotifers (e.g. *Lecane*, *Lepadella*). Only four records, all Victoria: billabongs of Goulburn, Mitta Mitta and Murray, and Ovens R. inlet to L. Mulwala: 15.0-17°C, pH 7.0-7.8, DO 8.0-9.8 mg l^{-1}, 65 μS cm^{-1}, 2 NTU.

Asplanchnopus multiceps Schrank
FIG. 15:2

Brachionus multiceps Schrank, 1793, p. 30, Fig. 3:16-19.
Asplanchnopus multiceps: De Guerne 1888, p. 57.

Type locality: (Germany).

Description: Saccate body, foot short, gradually merging into trunk; head margins sometimes reddish-coloured; vitellarium horseshoe-shaped with many nuclei; >50 pairs of protonephridial flame cells; large bladder; TR: rami slender, apices occasionally slightly cleft; one cerebral eye, two lateral ocelli; RE yellow-coloured, spinulate. Viviparous. Male large with remnants of digestive tract; many flame cells.

BL 445-1000 μm; male 400-500 μm; TR to 190 μm (FU 52 μm); RE 220-238 μm.

Distribution: Carnivore on other rotifers and small microcrustaceans (Koste 1987). More widespread than *A. hyalinus*: N.S.W., N.T., Qld, Vic.: 10.0-28.0°C, pH 6.0-8.1, DO 6.9-13.0, 37-170 μS cm^{-1}, <1-24 NTU.

Asplanchna Gosse
Asplanchna Gosse, 1850, p. 18

Body with thin transparent integument; saccate, tubular barrel- or bell-shaped, some species with lateral protrusions of the integument; corona an interrupted ciliary wreath, apical field large, more or less rounded; intestine and anus absent; ciliary bundles on relatively high papillae in apical field; one cerebral eye appended to brain; lateral antennae large, at beginning of posterior third of body; dorsal antennae paired; TR incudate, horizontal in mastax with apices facing posteriorly, everted and extruded to seize prey; oesophagus a wide extensible crop; kidney-shaped or spherical gastric gland on oesophagus. For a review of research on *Asplanchna*, see Koste (1978a). Seven species of *Asplanchna* are recorded from Australia.

Key to species of *Asplanchna* known from Australia

1. Rami clearly asymmetric under low magnification, left ramus with median inner tooth, lamellar plate behind ramus tip, right ramus without either . . . . . *A. asymmetrica* (Shiel & Koste)
   Rami symmetric under low magnification 2
2(1). Vitellarium spherical 3
   Vitellarium ribbon-like 4
3(2). Vitellarium with up to 8 nuclei; rudimentary foot glands absent; four pairs of protonephridial flame cells . . . . . *A. priodonta* Gosse
   Vitellarium with 12-15 nuclei; footglands present; 20-40 flame cells . . . . . *A. herrickі* De Guerne
4(2). Trophus without apophyses; constant 16 flame cells . . . . . *A. girodi* (De Guerne)
   Trophus with robust apophyses; 10-100 flame cells 5
5(4). Rami inner margin with distinct, large tooth 6
   Inner margin tooth absent or rudimentary . . . . . *A. intermedia* Hudson
6(4). Broad lamellae behind rami apices, which are symmetrical, acute; ca 32 nuclei in vitellarium; 10-20 flame cells; resting egg with vesicular structure . . . . . *A. brightwelli* (Gosse)
   Lamellae absent, apices asymmetric: left bifurcate, right single >50 nuclei in vitellarium; 40-100 flame cells; RE with pleated outer shell . . . . . *A. sieboldi* (Leydig)

Asplanchna asymmetrica Shiel & Koste comb. nov.
FIG. 15:3

Asplanchna brightwelli asymmetrica Shiel & Koste, 1985 pp. 9-11, Figs 4a, b.

Icenotype: Shiel & Koste (1985) Fig. 4a, b
Paratypes: South Australian Museum (SAM) V3945
Type locality: Solomon Dam, Palm Island, Qld.

Description: Body saccate; horseshoe-shaped vitellarium; TR asymmetrical: left ramus with short medial inner tooth, subterminal lamella and second uncus as in *A. brightwelli*, right ramus with none of these, more tapered and arched than that of *A. brightwelli*.

BL <500 μm; TR 130 μm.

Distribution: Carnivore/?omnivore in plankton of shallow waters. Collected in flooded Barmah Forest (by Kanella Fisheries staff) with *Trichocerca* trophi in gut. Rare, but probably more widely-distributed than limited records indicate. Known from Qld., Tas., Vic. W.A. 19.7°C, pH 7.3, 39 μS cm^{-1}, 2.1 NTU. May co-occur with *A. sieboldi*, markedly smaller than congener.

Comment: A. asymmetrica is readily separated from *A. brightwelli* on trophus structure alone, and trophus morphology is constant between widely separated populations. We consider *A. asymmetrica* specifically distinct from *A. brightwelli*.

Asplanchna brightwelli Gosse
FIGS 15:4, 16:b, 17:1,2

Asplanchna brightwelli Gosse, 1850, p. 23.

Type locality: (U.K.).
Description: Body usually saccate, some protrusions recorded by Gilbert (1973); TR: single small hollow tooth on scapus (distal inner ramus margin) (Fig. 17:1, 3); symmetrical squared-off lamellae behind tips of rami (Fig. 16b, 17:2); vitellarium with 21-33 nuclei; RE with semi-spherical lobes on surface. See Gilbert *et al.* 1979 for further details.

BL 500-1500 μm; Male 160-500 μm; RE 146-180 μm.
Distribution: Widely distributed on mainland Australia, not recorded from Tasmania. May be more widespread, likely to be confused with *A. sieboldi*. 9.1-26.0 °C, pH 7.0-8.3, DO 3.1-12.5 mg l^{-1}, 95-1000 μS cm^{-1}, <1-110 NTU.

Asplanchna girodi De Guerne
FIG. 18:1

Asplanchna girodi De Guerne, 1888, p. 54, Fig. 8.

Type locality: Azores.
Description: Repeatedly confused with *A. brightwelli;* body always saccate; outline of closed trophus somewhat rectangular; scapus usually without tooth, although some populations have been recorded with small teeth (Koste 1978a); apophysis rudiments also are known; male resembles that of *A. brightwelli*; RE covered with tightly-packed vesicles in a honeycomb pattern.

BL 500-700 μm; TR 93 μm; Male 250-397 μm.
Distribution: In plankton and littoral of pools, may be sympatric with *A. brightwelli*. Also in athallassic saline waters (Europe). Rare in L. Burley Griffin, ACT, R. Murray billabongs, and a single site near L. Wayatinah, Tas (Koste *et al.* 1988). 9.0-17 °C, pH 6.1-7.6, DO 10 mg l^{-1}, 65-203 μS cm^{-1}, 92 NTU.

Asplanchna herricki De Guerne
FIG. 18:2

Asplanchna herricki De Guerne, 1888, p. 52, Fig. 6.

Type locality: Azores.
Description: Body saccate; size and shape of both sexes

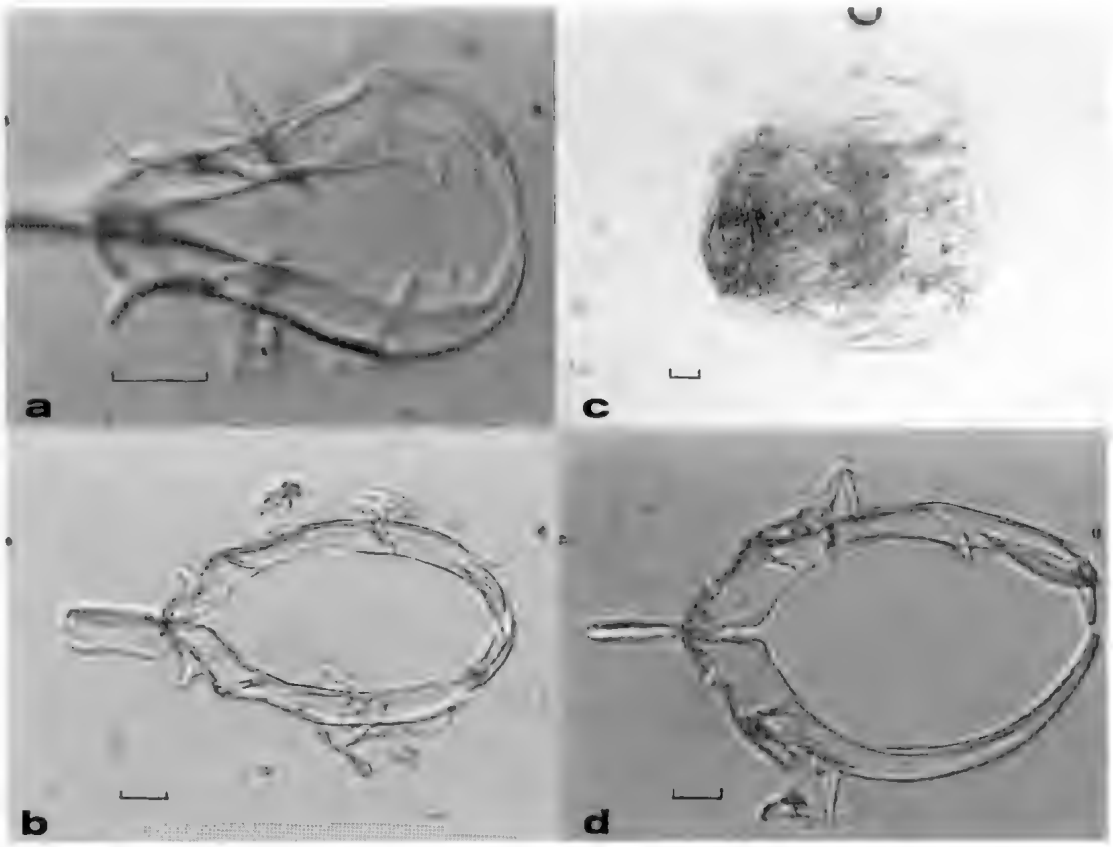


Fig. 16: a, *Asplanchna priodonta* Gosse, trophus. b, *A. brightwelli* Gosse, trophus. c, *A. symmetrica* Shiel & Koste, contracted, with *Keratella* prey in gut. d, trophus. Sony CVP G-700 video prints. Scale bars: 50μm adult; 10μm trophi.

resemble *A. priodonta*. Paired foot gland rudiments present; double projection at opening of secretory canal from them; 12-50 flame cells; TR: distinctive spatulate ramus; variability in size and shape of numerous inner rami teeth and presence or absence of unci; fulcrum short; rami tripartite; segmented by fillets; between upper and middle part, a large rounded lamella; manubria long, forklike rods; RE fully covered with vesicles.

BL 500-2000 μm; TR 110-120 μm; male 200-350 μm.

Distribution: Pelagic in oligotrophic pools and mesotrophic lakes in Europe and N America. Reported by Evans (1951) from Albert Park, Vic. and a single record in our collections (08.X.81) from a shallow creek draining L. Muir, W.A. 15.5°C, 3500 μS cm^{-1}.

Asplanchna intermedia Hudson
FIG. 18:3

Asplanchna intermedia Hudson, in Hudson & Gosse, 1886, p. 122.

Type locality: (U.K.)

Description: Saccate or polymorphic body; vitellarium with 44-48 nuclei; TR: generally slender morphology;

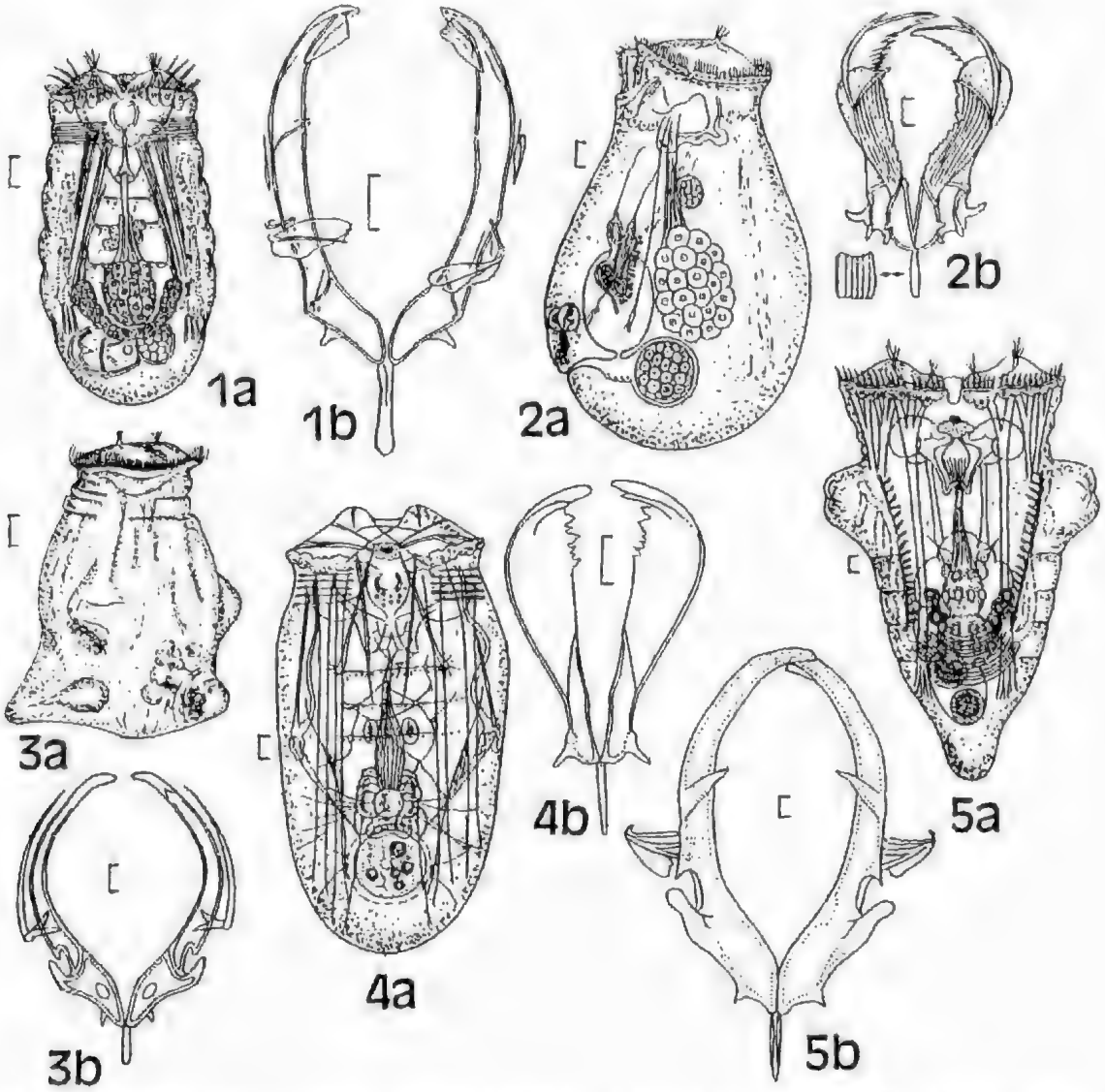


Fig. 17: 1, *Asplanchna girodi* (De Guerne): (a) dorsal; (b) trophus. 2, *A. herricki* De Guerne: (a) dorsal; (b) trophus, lateral view of fulcrum on left. 3, 4, *intermedia* Hudson (a) dorsal; (b) trophus. 4, *A. priodonta* Gosse: (a) dorsal; (b) trophus. 5, 4 *sieboldi* (Leydig): (a) dorsal; (b) trophus. 1a after Wang (1961), 1b after De Beauchamp (1951), 2 after Wulfert (1961), 4a, 5a after Hudson & Gosse (1886), 4b after Hauer (1952), 5b after Hauer (1937). Scale bars: adults 50 μm, trophi 10 μm

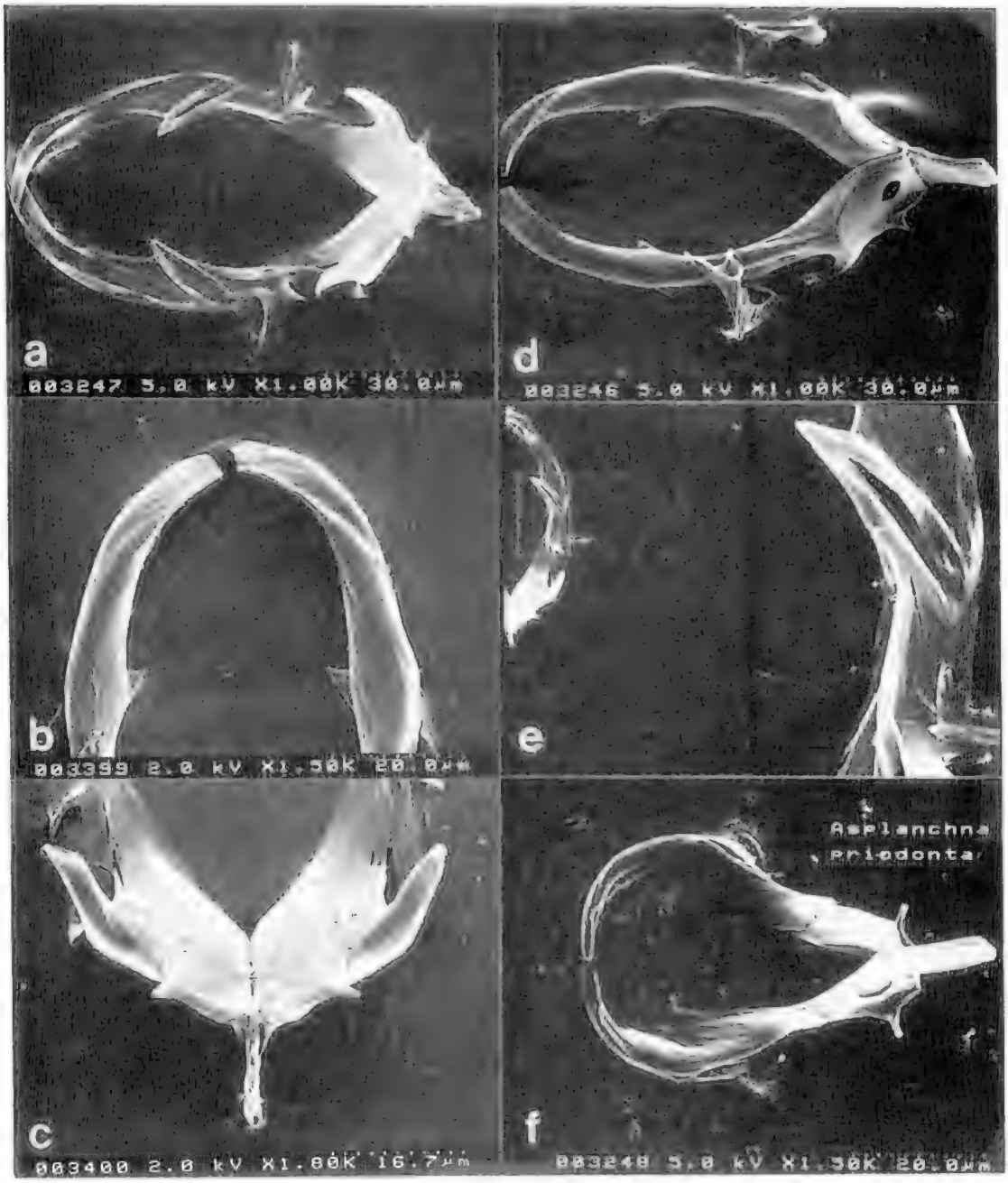


Fig. 18. 1, *Asplanchna brightwelli* Gosse trophus, ventral. 2, trophus, dorsal. 3, detail of tooth on inner ramus. 4, *A. priodonta* Gosse: trophus, dorsal. Scanning electron micrographs, Kodak T-Max, Hitachi SEM, University of Waikato, Hamilton, N.Z.

rami tips resemble those of *A. sieboldi*, albeit less robust and less noticeable bifurcate; well-developed apophyses; rami not lamellate, and no inner tooth on scapus; RE with anastomosing ridges.

BL 580-900 μm; TR 104-156 μm; male 290-439 μm; RE 136 μm.

Distribution: In pelagial of ponds and lakes (Europe). Single early record from Qld (Colledge 1914). Not seen in our samples, needs verification.

Comment: Some similarities with *A. brightwelli* (apophyses on the rami) and *A. girodi* (absent or reduced scapus teeth), however the specific distinction of this taxon was verified by the study of Gilbert *et al.* (1979).

Asplanchna priodonta Gosse
FIGS 16a, 17:4, 18:4

Asplanchna priodonta Gosse, 1850, p. 18, Figs 1, 2

Type locality: Hyde Park, U.K.

Description. Body rounded to saccate, often with a single hump on one side at the posterior; TR: distinctive spatulate proximal rami, with denticulate inner tip (Fig. 16a, 18:4b); no tooth on scapus; rami external margins from hemispherical curve, tapering to small, projecting (almost right angled) subapophysis; RE reported to be smooth-shelled.

BL 250-1500 μm; male 200-500 μm; Tr 60-80 μm; RE 127-150 μm.

Distribution: Cosmopolitan, perennial in oligotrophic lakes, also in brackish water (Europe). Reasonably common in billabongs, reservoirs and rivers of eastern mainland Australia, not recorded from Tasmania, N.T. or W.A. 7.9-27.0°C, pH 7.4-8.2, DO 8.6-12.5 mg l^{-1}, 46-850 μS cm^{-1}, <1-120 NTU.

Asplanchna sieboldi (Leydig)
FIG. 18:5

Notommata sieboldi Leydig, 1854, p. 24, Fig. 2: 15-17.
Asplanchna sieboldi: Eyferth 1878, p. 94.

Type locality: (Germany).

Description: Resembles *A. brightwelli*, commonly larger. Transitional forms are recorded (Koste 1978). Variable morphology: saccate, cruciform or bell-shaped. TR: superficially similar to those of *A. brightwelli*, but lacking lamellae, and asymmetric (left ramus bifurcate, right single with the tip fitting between the left apices when closed). Vitellarium with 55-96 nuclei, RE covered with elevated concave discs. Male corresponds to female in morphological variability.

BL 500-2500 μm; male 300-1200 μm; TR 80-90 μm (Europe), 220-340 μm (Murray-Darling billabong populations, Koste & Shiel (1980)); RE ca. 200 μm.

Distribution: Cosmopolitan warm stenotherm, most common *Asplanchna* in our collections, not yet recorded from W.A. May be the largest planktonic carnivore in pelagic communities, particularly in billabongs, where it preys on other rotifers and small microcrustaceans. 7.0-25.3°C, pH 6.9-8.5, DO 1.7-11.3 mg l^{-1}, 27-1100 μS cm^{-1}, <1-50 NTU.

Comment: There has been considerable confusion in the literature between *A. sieboldi* and *A. brightwelli*, despite the clarification by Gilbert *et al.* (1979). The two taxa are readily separated on trophi structure, also by vitellarium nuclei number.

Biogeography

To date we have accumulated some 5000 microfaunal samples from scattered parts of mainland Australia and Tasmania. The area covered probably represents less than a fraction of 1% of the continent. Virtually every sample series we examine contains new species or new records (cf. Storey *et al.* 1993). Comments on biogeography thus are still preliminary and reflect the small number of collectors.

At the completion of this series we will have reviewed more than 664 rotifer taxa presently known from the continent (515 Monogononta, 84 Digononta and 66 subspecies or infrasubspecific variants). We suspect that this represents less than half, possibly less than a third, of the Rotifera which ultimately will be found here. Of these, 60 taxa (10%) at the species level are known only from Australia, with a further approx. 5% of taxa at subspecies or 'varietal' resolution apparently indigenous. Some of these will be resolved in the on-going global revision, e.g. at least two subspecific or unresolved taxa from our earlier papers have been elevated to specific rank by revisers (Segers, in press; De Smet, in press).

Conversely, some taxa we thought to be endemic to Australia have been found recently in New Zealand (Sanoamuang & Stout 1993) and another, *Lepadella williamsi* Koste & Shiel, 1980, was declared a synonym of *L. vandenbrandei* Gillard, 1952 by Segers (1993). In any event, the level of endemicity of the Australian Rotifera lies somewhere between 10-15% at present the highest proportion for any continent on present information.

Acknowledgments

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Zealand Limnological Society provided a travel grant, which enabled collections to be made on the South Island. Garth Watson at MDFRC provided technical and field support in collection, sorting and preliminary identifications, and developed the rapid trophi-preparation method used for the SEM work. For their help in the search for *Synchaeta jollyi*, thanks to Larelle Fabbro (University of Central Queensland, Rockhampton) and Yoshi Kobayashi (Australian Water Technologies, Science & Environment, Sydney). We thank Dr Alice Wells for her critical review of this manuscript which has resulted in a greatly improved paper.

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XYSTRIDURA AND OTHER EARLY MIDDLE CAMBRIAN TRILOBITES FROM YAXIAN, HAINAN PROVINCE, CHINA

BY R. J. SHIEL & W. KOSTE†*

Summary

Xystridurine trilobites are an important element of early Middle Cambrian faunas of Australia, China and Antarctica. An early Middle Cambrian trilobite fauna is described from the Damao phosphate mine of the Yaxian district, Hainan Province, People's Republic of China. These include *Pagetia luoyacunensis* sp. nov., *Xystridura hainanensis* Sun, 1963, *X. yaxianensis* Zhu & Lin, 1978, *X. orientalis* Zhu & Lin, 1978, *Galahetes hainanensis* Zhu & Lin, 1978 and *Kootenia* sp. The species of *Xystridura* are described in considerably more detail than previously possible due to the discovery of new material particularly pygidia. It is suggested that the three subgenera of *Xystridura* erected by Öpik (1975) are of doubtful value. *Galahetes pyrus* Zhu & Lin, 1978 is placed in synonymy with *G. hainanensis.*

KEY WORDS: Middle Cambrian trilobites, China, Australia, *Xystridura, Galahetes.*

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XYSTRIDURA AND OTHER EARLY MIDDLE CAMBRIAN TRILOBITES FROM YAXIAN, HAINAN PROVINCE, CHINA

by LIN TIAN-RUI* & J. B. JAGO†

Summary

LIN, TIAN-RUI & JAGO, J. B. (1993) *Xystridura* and other early Middle Cambrian trilobites from Yaxian, Hainan Province, China. *Trans. R. Soc. S. Aust.* 117(3), 141-152, 30 November, 1993.

Xystridurine trilobites are an important element of early Middle Cambrian faunas of Australia, China and Antarctica. An early Middle Cambrian trilobite fauna is described from the Damao phosphate mine of the Yaxian district, Hainan Province, People's Republic of China. These include *Pagetia luoyaoensis* sp. nov., *Xystridura hainanensis* Sun, 1963, *X. yaxianensis* Zhu & Lin, 1978, *X. orientalis* Zhu & Lin, 1978, *Galahetes hainanensis* Zhu & Lin, 1978 and *Kootenia* sp. The species of *Xystridura* are described in considerably more detail than previously possible due to the discovery of new material particularly pygidia. It is suggested that the three subgenera of *Xystridura* erected by Öpik (1975) are of doubtful value. *Galahetes pyrus* Zhu & Lin, 1978 is placed in synonymy with *G. hainanensis*.

KEY WORDS: Middle Cambrian trilobites, China, Australia, *Xystridura*, *Galahetes*.

Introduction

Xystridura is an important early Middle Cambrian trilobite genus which is known from the Northern Territory (Öpik 1975), Queensland (Whitehouse 1939; Öpik 1975), South Australia (Gatehouse 1986), and western New South Wales (Wopfner 1966; Öpik 1968, 1975). *Xystridura templetonensis* is one of the nominate species of the *Xystridura templetonensis/Redlichia chinensis* Zone of the early Middle Cambrian of northern Australia. *Xystridura* was known only from Australia prior to its discovery on Hainan Island, China (Sun 1963). It is now known from elsewhere in China (e.g. Zhou *et al.* 1982) as well as Antarctica (e.g. Palmer & Gatehouse 1972). Öpik (1975) described a second member of the Xystridurinae, *Galahetes*, from the early Middle Cambrian of Queensland; it has since been recorded from Hainan (Zhu & Lin 1978) and Gansui, northeast China (Zhou *et al.* 1982). McNamara (1981) discussed the evolution of the Middle Cambrian xystridurine trilobites from northern Australia.

The purpose of this paper is to revise the work of Sun (1963) and Zhu & Lin (1978) and to describe the trilobites (including species of both *Xystridura* and *Galahetes*) from the *Xystridura* Zone of the early Middle Cambrian Damao Formation from the Damao phosphate mine of the Yaxian district, Hainan Province, People's Republic of China (Fig. 1). The area contains some of the most important phosphate deposits in China. As listed below the Damao Formation is richly fossiliferous and includes trilobites, bradoriids, brachiopods, bivalves, hyoliths, microfossils, etc. Data on the trilobites have been previously published by Sun (1963) and Zhu & Lin (1978). The present material, which was collected by Lin Tian-Rui in 1987, 1988 and 1991 provides extra specimens which give a better understanding to the previously described species. In particular, it has allowed the pygidia of the various species of *Xystridura* to be identified, which is important because the pygidium provides one of the key features in separating the different species of *Xystridura*. In addition this paper provides stratigraphic information on the distribution of trilobites which was not given in the papers of Sun (1963) and Zhu & Lin (1978).

The stratigraphic section at Damao as described by Zhang Xiguang (1986), and revised in this paper, is given in descending order as follows:

Damao Formation (top and bottom not exposed)

12. Grey thin to medium-bedded siliceous rock intercalated with silty and muddy shale, containing brachiopod fragments. 12.1m
11. Grey and yellowish grey thin to medium-bedded micaceous siltstone intercalated with a few siliceous shale beds, yielding bradoriids: *Houlongdongella disulcata* Loc, *H. sphaerica* Zhang, *Ophiosema strumatum* Zhang, *O. sicyoideum* Zhang, *Ophiosema (Sinophiosema) chinense* Zhang, *O. (S.) transversum* Zhang, *O. (S.) deliatum* Zhang, *O. (S.) paradoxum* Zhang, *Guangdongella obesa* Zhang and the brachiopod *Lingulella liui* Sun. 1.2m
10. Dark grey medium-bedded siliceous siltstone, bearing the trilobite *Xystridura* sp. 6.1m
9. Greyish white and greyish yellow thin to medium-bedded siliceous siltstone intercalated with silty and

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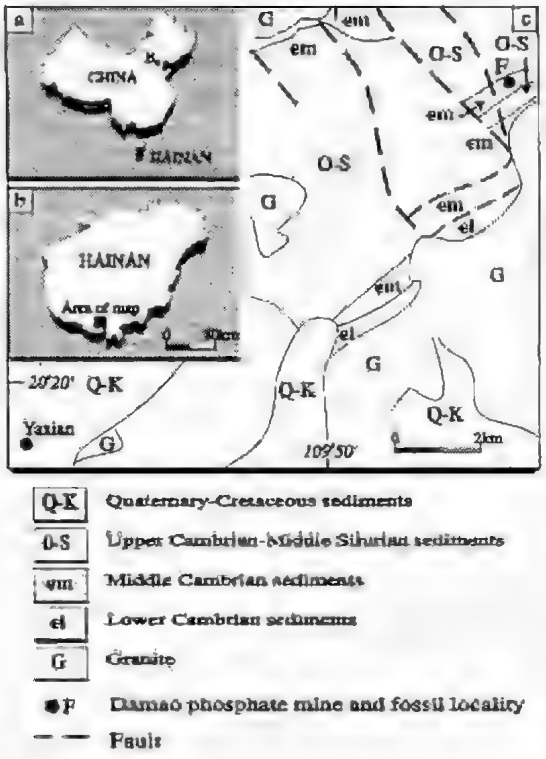


Fig. 1. Locality map. In box A, B indicates Beijing.

muddy shales, containing the bradoriids *Ophiosema subrotundum* Zhang and *Mannocosmia* sp.; the trilobites *Xystridura hainanensis* Sun, *X. yaxianensis* Zhu & Lin, *X. orientalis* Zhu & Lin and *Galahetes hainanensis* Zhu & Lin; brachiopods *Lingulella tangshihensis* Resser & Endo and *Acrothele* sp. 2.5m

8. Greyish yellow siliceous shale intercalated with thin to medium-bedded siliceous siltstone and containing trilobites *Xystridura orientalis* Zhu & Lin and *Pagetia luoyacunensis* sp. nov. 5.3m
7. Greyish white and grey medium-bedded siltstone and siliceous shale, containing the bradoriids: *Houlongdongella disulcata* Lee, *H. inflata* Zhang, *Yaxianella sulcata* Lin, *Y. punctata* Zhang, *Ophiosema strumatum* Zhang, *O. subrotundum* Zhang, *Indota acuta* Zhang, *Guangdongella obesa* Zhang, *Mannocosmia torquata* Zhang, *Plesidielymella* sp., *Bradoria* sp.; trilobites *Xystridura hainanensis* Sun, *X. orientalis* Zhu & Lin, *Galahetes hainanensis* Zhu & Lin, *Kootenia* sp. and *Pagetia luoyacunensis* sp. nov.; brachiopods *Lingulella tangshihensis* Resser & Endo, and *Homotreta* sp. 5.2m
6. Dark grey siliceous shale and phosphatic siliceous rock intercalated with dark grey phosphorite, containing the bradoriid *Indota acuta* Zhang; the trilobites *Xystridura hainanensis* Sun, *X. orientalis* Zhu & Lin, and *Pagetia luoyacunensis* sp. nov. 9.6m
5. Dark brown nodular manganese ore bed (thickness about 2m), with siliceous shale at the base, yielding brachiopod fragments. 2.6m
4. Greyish white and dark grey medium to thick bedded siliceous siltstone and quartzose sandstone intercalated with dolomite and a few micaceous muddy shales. 42.2m
3. Greyish green and greenish red medium and thin bedded micaceous siltstone intercalations. 55.8m
2. Greyish white massive quartzose sandstone and siliceous siltstone intercalated with a few medium to thick-bedded dolomite horizons. 8.3m
1. Greyish white massive medium-grained quartzose sandstone. 35.8m

Age and affinities of fauna

The trilobites described herein comprise the following species *Pagetia luoyacunensis* sp. nov., *Xystridura hainanensis* Sun, *X. yaxianensis* Zhu & Lin, *X. orientalis* Zhu & Lin, *Galahetes hainanensis* Zhu & Lin, and *Kootenia* sp. In China *Xystridura* and *Galahetes* are known from the Tianshan (Wang *et al.* 1985) and from Gansu (Zhou *et al.* 1982). The age here is equivalent to the Maozhuangian Stage of the North China biostratigraphic scheme. In Australia *Xystridura* and *Galahetes* are important members of the early Middle Cambrian fauna of Australia (Öpik 1975). The various species of *Xystridura* described by Öpik (1975) are either of Ordian or Templetonian age. In Australia *Xystridura* is known from the Northern Territory (Öpik 1975), Queensland (Whitehouse 1939; Öpik 1975), western New South Wales (Wopfner 1966; Öpik 1968, 1975) and from the Kalladeina Formation of the Warburton Basin in northeastern South Australia (Gatehouse 1986). In Australia *Galahetes* has been recorded from the Templetonian of the Duchess area (Öpik 1975). *Xystridura* has also been described from early Middle Cambrian rocks of Antarctica (Palmer & Gatehouse 1972; Soloviev & Grikurov 1979). In summary members of the Xystriduridae are an important element of the very early Middle Cambrian faunas of Australia, Antarctica and China.

The specimens described herein show some tectonic distortion. They are deposited at either the Nanjing Institute of Geology and Palaeontology, Academia Sinica (NIGP) or the Department of Earth Sciences, Nanjing University (NUESD). All figured specimens were whitened with magnesium oxide prior to photography.

Systematic descriptions

Suborder EODISCINA Kobayashi, 1939
Family PAGETHIDAE Kobayashi, 1935
Genus PAGETIA Walcott, 1916

Synonymy: See Jell 1975, p. 30.
Type Species: Pagetia bootes Walcott, 1916, p. 408, Pl. 67, Figs 1, 1a-f.
Diagnosis: See Jell 1975, p. 30.

Pagetia luoyacunensis sp. nov.
FIGS 2a-f, 6d.

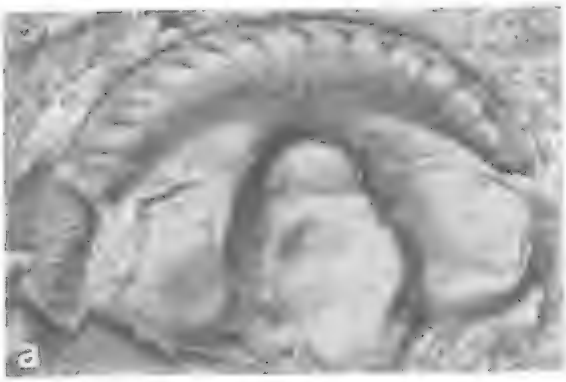
Dawsonia dawsoni: Sun 1963 p. 610, Pl. 1, Figs 7, 7a.
Pagetia sp. Zhu & Lin 1978 p. 439, Pl. 1, Fig. 1.

Material: 11 cranidia and nine pygidia.
Etymology: After the nearby town of Luoyacun.
Holotype: The cranidium (NUESD 210), Fig. 2b, is chosen as the holotype.
Diagnosis: Member of *Pagetia* with anteriorly tapered glabella; cranidial spine has length about two-thirds that of glabella; shallow transglabellar furrow close to glabellar anterior; wide fixed cheeks; palpebral lobes extend from opposite transglabellar furrow to opposite anterior of spine; well-developed palpebral furrows; short (sag.), strongly depressed preglabellar field; wide border; 16-20 cephalic border scrobicules stop just short of margin. Pygidium with gently tapering axis which stops just short of posterior margin. Axis comprises four axial rings and terminus. Each axial ring and terminus bears spine base. Pleural areas with three pairs of pleural furrows; narrow border. Faintly pustulose surface ornament.
Description: Cranidium with anteriorly tapered glabella, length about 0.6-0.65 that of cranidium; shallow transglabellar furrow placed close to well-rounded glabellar anterior. Well-developed cranidial spine, length about two thirds that of glabella; Axial furrows deep, wide; baculae absent. Wide fixed cheeks, palpebral lobes extend from opposite transglabellar furrow to opposite anterior of spine; well-developed palpebral furrows; narrow but distinct eye ridges meet axial furrows just forwards of transglabellar furrow. Short, strongly-depressed preglabellar field; wide anterior border furrow not crossing lateral border. Wide border with 16-20 radial scrobicules which stop just short of margin. Wide, deep posterior border furrow.
Semicircular pygidium. Axis tapers gradually rearwards; it extends almost to posterior margin. Axis comprises four axial rings and terminus. On available specimens each axial ring bears spine base as does terminus. Semi-elliptical articulating half-ring. Pleural areas contain three pairs of pleural furrows. Narrow shallow border furrow; narrow border. Both cranidium and pygidium have finely pustulose surface ornament.
Discussion: Prior to the specimens described herein, this species was known from only the two very poorly preserved cranidia figured in Sun (1963, Pl. 1, Figs 7, 7a) and Zhu & Lin (1978, Pl. 1, Fig. 1). Although somewhat distorted the available material indicates that it should be the basis of a new species. Of the Australian species of *Pagetia* described by Jell (1975), the new species *P. luoyacunensis* is probably closest to *P. howardi* Jell. The cranidia of the two species are quite similar, although the cephalic border of *luoyacunensis* is wider than that of *howardi*. The pygidial axis of *luoyacunensis* is wider than that of *howardi*.

P. luoyacunensis differs from the type species of *Pagetia*, *P. bootes* Walcott (e.g. see Rasetti 1966, p. 504, Pl. 59, Figs 11-13), in that *P. bootes* has a wider and shallower preglabellar field, a longer and more slender cranidial spine, a narrower pygidial axis with five axial rings plus a terminus bearing a long spine and a smoother pleural field. There are some similarities between *P. luoyacunensis* and *P. quebecensis* Rasetti (1966, p. 506, Pl. 59, Figs 5-10) but *P. luoyacunensis* differs from *P. quebecensis* in having small palpebral lobes, in having distinct baculae and in not having pronounced spine bases on the pygidial axis.

Order REDLICHIDA Richter, 1933
Suborder REDLICHIINA Harrington, 1959
Superfamily PARADOXIDACEA Hawle & Corda, 1847
Family CENTROPLEURIDAE Angelin, 1854
Genus XYSTRIDURA Whitehouse, 1936

Type Species: Xystridura templetonensis (Chapman) — *Milesia templetonensis* Chapman, 1929, p. 214, Pl. 22, Fig. 19, refigured by Whitehouse 1939, Pl. 21, Fig. 10 (see also comments by Palmer & Gatehouse 1972, p. 13).
Diagnosis: See Öpik 1975, p. 20, 31.
Discussion: Öpik (1975) discussed *Xystridura* in some detail. He suggested that there should be at least three subgenera in *Xystridura*, i.e. *X. (Xystridura)*, *X. (Polydinotes)* and *X. (Inosacotes)* with the type of *X. (Xystridura)* being *X. templetonensis*. In his differential diagnosis Öpik (1975, p. 31) states "In *Inosacotes* and *Polydinotes* the cephalic test is strongly ornamented, the thorax expands rearwards, the pygidial axial lobe is fused with the thorax, and the pygidial margin is visibly denticulate; furthermore in *Polydinotes* the pleural tips are bispinose (simple in *Xystridura* and *Inosacotes*) and in *Inosacotes* the anterior facial sutures are fused (functional in *Xystridura* and *Polydinotes*)".
It should be noted that species included by Opik in *X. (Xystridura)* also show a thorax which expands rearwards, e.g. *X. milesi* (see Öpik 1975, Pl. 14, Fig. 2), and *X. carteri* (see Öpik 1975, Pl. 15, Fig. 1). The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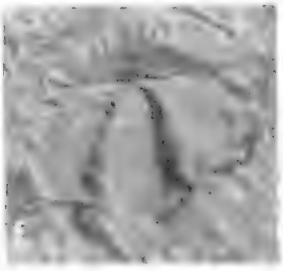
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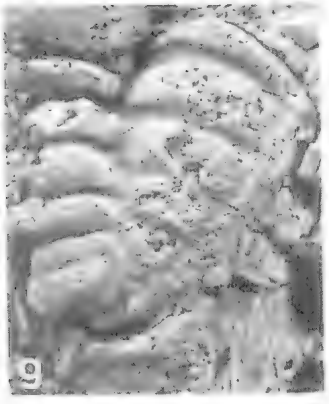
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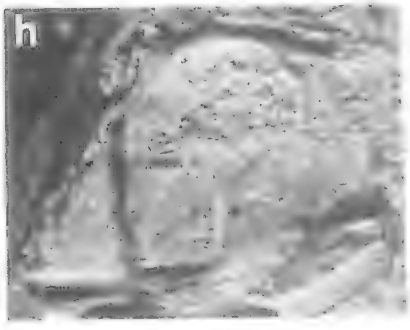
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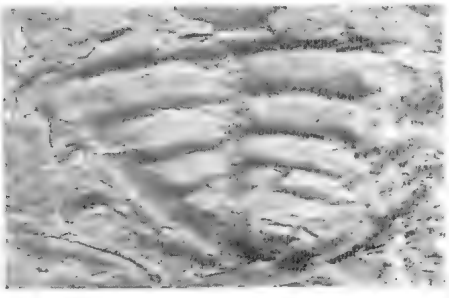


present authors do not regard the caecal patterns shown in the species of *Iunsacotes* and *Polydinotes* as being of subgeneric taxonomic significance. This plus the variations allowed for by Öpik would suggest that his subgeneric groupings may be of doubtful value.

Xystridura hainanensis Sun, 1963
FIG. 3a-h

Xystridura hainanensis Sun, 1963 p. 608, Pl. 1, Figs 1-4; Zhu & Lin 1978 p. 440, Pl. 1, Figs 2, 3 (non 4a, 4b).

Material: Twenty cranidia and eight pygidia.

Lectotype (designated herein). The pygidium figured by Sun (1963, Pl. 1, Figs 4, 4a) is selected as lectotype. Sun did not erect a holotype.

Diagnosis: Species of *Xystridura* in which glabella extends almost to anterior border furrow; glabella anterior broadly rounded. Long palpebral lobes extend from opposite anterior of occipital ring to just forwards of 3p furrows. Anterior end of palpebral lobe almost meets axial furrow. Pygidium with short axis; with four axial rings and a terminus. Two pairs of marginal spines; very long, slender anterior pair directed posterolaterally at an angle of about 45°; second pair short.

Description: Cranidium wide (tr.), slightly convex, with a length about two-thirds the width between palpebral lobes. Glabella extends almost to anterior border furrow; preglabellar field very short (sag.) but clearly separates preglabellar furrow from anterior border furrow; glabellar length about 0.85 that of cranidium. Glabella has slight waist at 1p furrows; widest just forwards of 3p furrows; broadly rounded glabellar anterior. Narrow axial furrow of moderate depth. Three pairs of lateral glabellar furrows. Each 1p furrow is directed slightly to posterior and extends about 0.4 of distance across glabella; 2p furrows almost horizontal; 3p furrows slightly arcuate with convexity to anterior. 3p furrows, slightly convex anteriorly, set in from axial furrow and not connecting with it. Narrow occipital furrow deepest abaxially. Occipital ring widest centrally; small median node. Long palpebral lobes extend from opposite anterior of occipital ring to just forwards of 3p furrows. Palpebral furrow very shallow, barely discernible on many specimens. Palpebral areas of fixigenae wide and flat; at posterior end width 0.5-0.6 that of glabella; anterior end narrow where anterior of palpebral lobe almost meets axial furrow. Anterior areas of fixigenae almost flat. Preocular sections of facial suture diverge markedly. Very short postocular sections of facial suture diverge slightly. Wide anterior border with shallow terrace lines; narrow anterior border furrow. Shallow posterior border furrow. Very narrow posterolateral border.

Pygidium very wide (tr.) with length about half width. Short axis extends just over half length of pygidium. Axis has four axial rings plus terminus. Wide pleural field with at least two pairs of pleural furrows and two pairs of interpleural furrows. Two pairs of marginal spines. Anterior pair arise from first pleurae of pygidium; very long slender spines with wide base; directed posterolaterally at angle of about 45°. Second pair short, pointed with wide base. It is possible that there is a very short third pair of spines but this is difficult to determine on available material.

Discussion: The pygidia shown by Zhu & Lin (1978, Pl. 1, Figs 4a, b) as belonging in *X. hainanensis* are now placed in *X. orientalis*. When compared with the Australian species described by Öpik (1975) *X. hainanensis* is probably closest to *X. fracta* in that the cranidia are quite similar. The pygidia are similar in terms of lengths of pygidial axis but differ in the presence of the longer spines in *X. hainanensis* and in the nature of the pygidial pleural and interpleural furrows.

The anterior pygidial spines of *hainanensis* are longer than in any other species of *Xystridura* with the possible exception of *X. glacia* Palmer & Gatehouse, 1972. However, *glacia* has three relatively narrow pygidial spines whereas *hainanensis* has two spines, each with a large base. The anterior pygidial spine of *X. glacia* at its distal end is directed approximately parallel to the axis; this is not so in *X. hainanensis*, even allowing for tectonic distortion.

Xystridura yaxianensis Zhu & Lin, 1978
FIG. 4a-e.

Xystridura yaxianensis Zhu & Lin, 1978 p. 440, Pl. 1, Figs 5-6.

Xystridura orientalis Zhu & Lin, 1978 p. 441, Pl. 1, Fig. 8 only.

Material: One specimen comprising the cranidium, the right librigena, most of the thorax and the pygidium; 14 cranidia and four pygidia. None is well preserved.

Holotype: The cranidium (NIGP 44903) figured by Zhu & Lin (1978, Pl. 1, Fig. 5) and refigured here as Fig. 4d.

Fig. 2. a-f, *Pagetia luoyacunensis* sp. nov. a, NUESD 207, cranidium x20; b, NUESD 210, holotype cranidium, x20; c, NUESD 212, cranidium, x20; d, pygidium, x20; e, NUESD 214, pygidium, x20; f, cranidium (figured as *Pagetia* sp. by Zhu & Lin 1978, Pl. 1, Fig. 1), x20.
g-i, *Kootenia* sp. g, NUESD 218, partial pygidium, x5; h, NIGP 44916, partial cranidium (figured by Zhu & Lin 1978, Pl. 2, Fig. 8); i, pygidium, NUESD 219, x8.
All specimens are internal moulds.

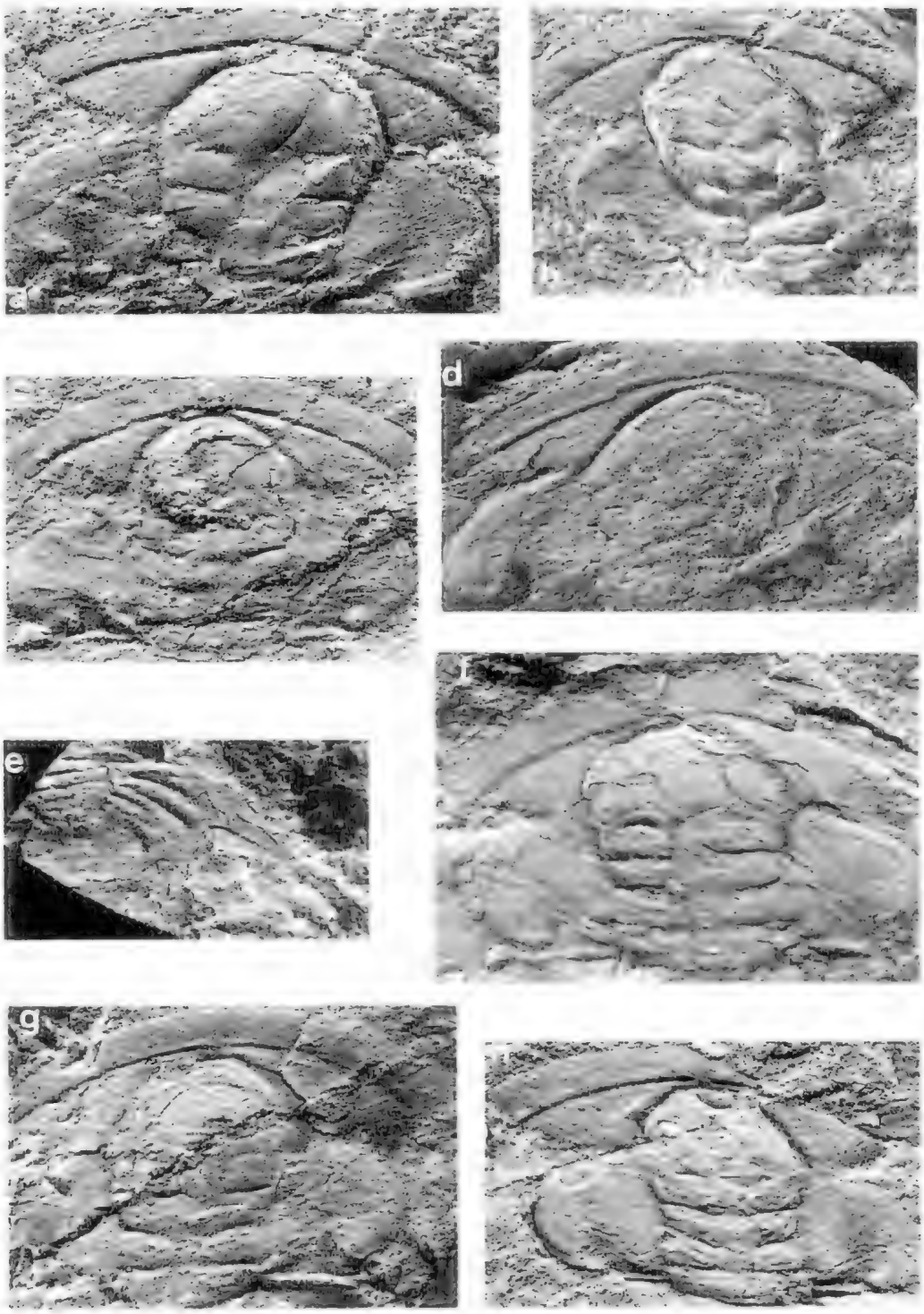


Fig. 3. *Xystridura hunanensis* Sun, 1963. a, NUESD 220, cranidium, x4; b, NUESD 217, cranidium, x4; c, NUESD 222, cranidium, x4; d, NUESD 225, cranidium, x4; e, NUESD 228, pygidium, x2.5; f, NUESD 221, cranidium, x2; g, NUESD 223, cranidium, x3.5; h, NUESD 224, cranidium, x3.
All specimens are internal moulds.

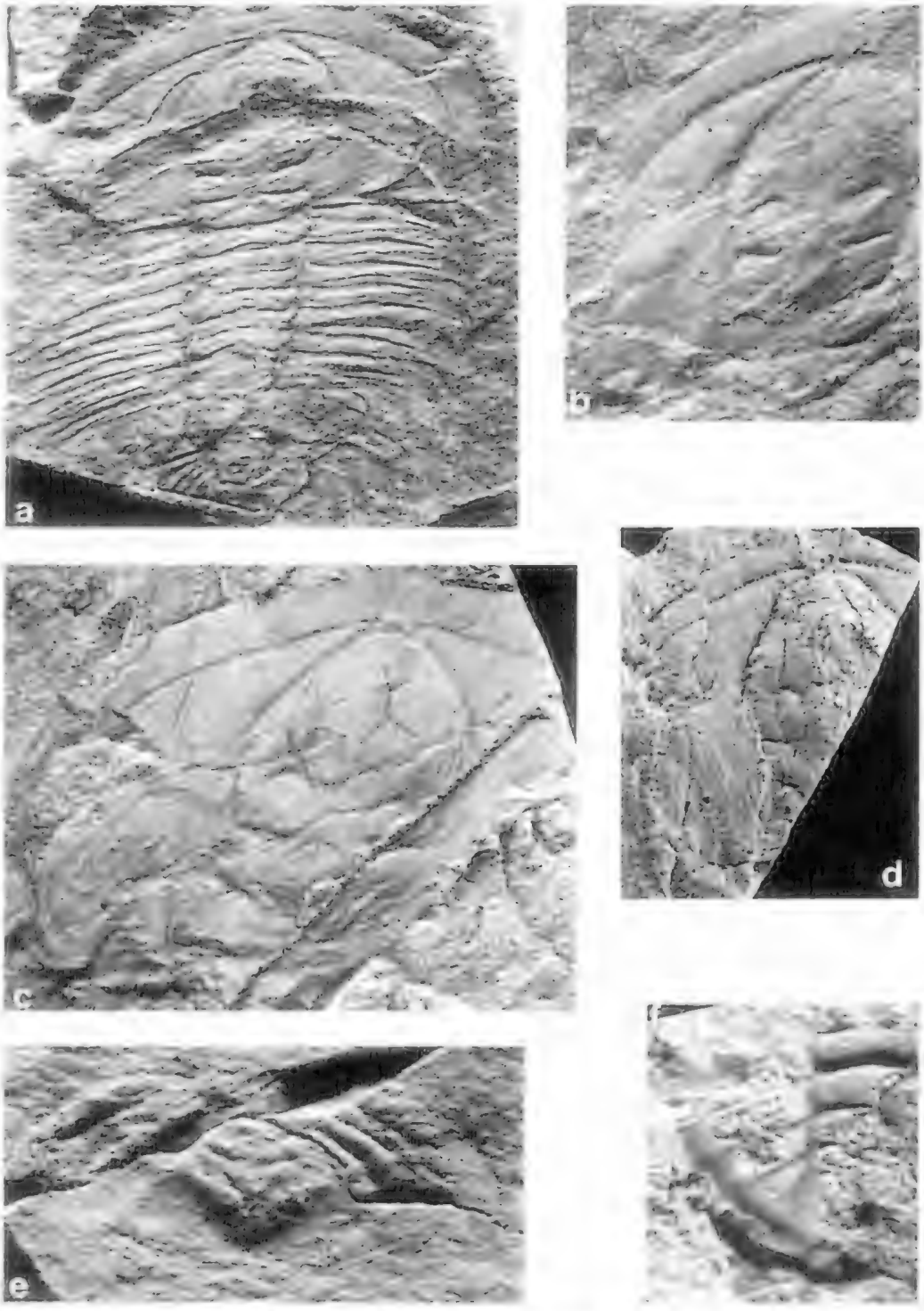
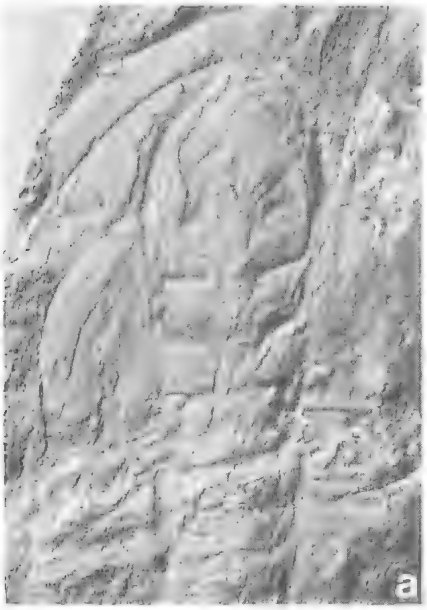


Fig. 4. a–e *Xystridura yaxianensis* Zhu & Lin, 1978. a, NUESD 229, almost complete specimen, rubber cast of external mould, x2; b, cranidium, rubber cast of external mould, x3; c, NUESD 234, cranidium, rubber cast of external mould, x3; d, NIGP, holotype cranidium (originally figured by Zhu & Lin 1978, Pl. 1, Fig. 5), internal mould, x2; e, NIGP 44906, pygidium, (originally figured by Zhu & Lin 1978, Pl. 1, Fig. 8 as belonging to *X. orientalis*), internal mould, x4. f, *Kootenia* sp., NIGP 44917, pygidium, (originally figured by Zhu & Lin 1978, Pl. 2, Fig. 9), internal mould, x5.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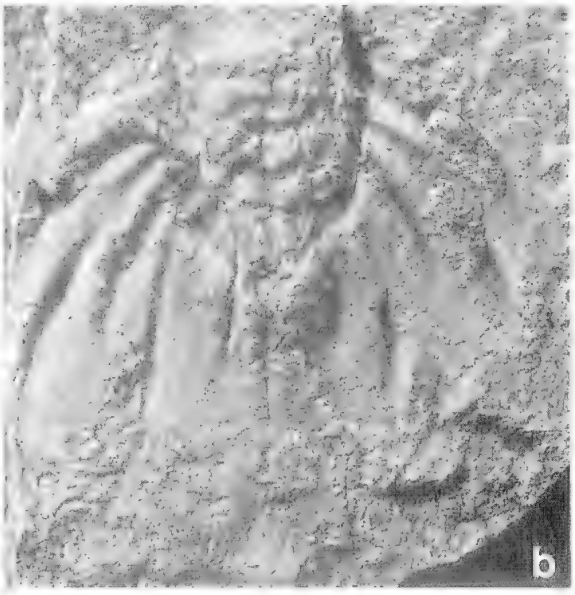
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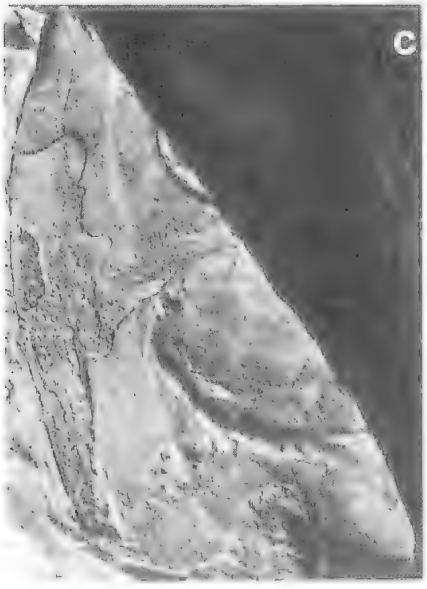
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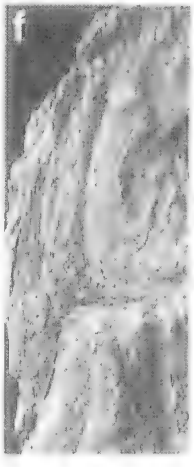
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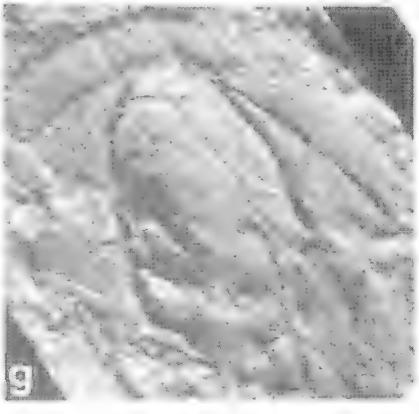
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Diagnosis: Species of *Xystridura* in which glabella extends almost to anterior border. Sharply rounded glabellar anterior. Short pygidial axis. Three pairs of pygidial spines. Moderately long, anterior pair with wide base directed outwards and backwards; second shorter pair extend inwards and backwards; third pair very short. Central posterior margin of pygidium broadly curved to anterior.

Description. Cephalon semi-circular. Glabella extends almost to anterior border furrow; length about 0.85-0.9 that of cranidium. Glabella with slight waist at about 2p furrows; widest just anterior to 3p furrows. Glabellar anterior sharply rounded. Narrow axial furrow of moderate depth. Three pairs of lateral glabellar furrows. Each 1p furrow directed slightly to posterior; they almost meet abaxially; 2p furrows almost horizontal; 3p furrows which do not meet the axial furrow slightly arcuate with convexity to anterior. Both palpebral and anterior sections of fixigenae almost flat. Narrow occipital furrow. Occipital ring widest abaxially; faint occipital node. Long palpebral lobes extend from opposite occipital ring just anteriorly of 3p furrows. Shallow palpebral furrow. Preocular sections of facial suture diverge markedly. Narrow shallow anterior border furrow; wide anterior border with faint terrace lines on some specimens. Shallow posterior border furrow; very narrow posterolateral border. Poorly preserved librigena with narrow shallow border furrow; wide border extends into genal spine of indeterminate length. Thorax of 12 segments. Shallow axial furrows. Width of axis about 0.6 that of pleural regions. Axis parallel sided from first to fifth segment gradually narrowing posteriorly. Pleurae almost flat; pleural furrows narrow abaxially but continue as shallow furrow into well-developed posteriorly directed pleural spines.

Available pygidia poorly preserved. Axis comprises four axial rings plus terminus. Wide pleural field with at least two pairs of pleural furrows and two pairs of interpleural furrows. Wide flat border with faintly-developed terrace lines. Three pairs of marginal spines. Anterior pair extending from first pleural segment of pygidium; of moderate length with wide base and extending posterolaterally. Second shorter pair extending posteromedially. Third pair very short; more change of slope in pygidial margin than distinct spines. Central posterior margin broadly curved to anterior.

Discussion: When compared with the species described by Öpik, *X. yaxianensis* is closest to *X. templetonensis*. However the cranidium of *yaxianensis* has a more sharply rounded glabellar anterior and longer palpebral lobes than *templetonensis*. *X. yaxianensis* differs from *X. hainanensis* in having a more sharply rounded glabellar anterior and a longer pygidial axis. The pygidial spines in the two species are quite different.

The pygidium (NIGP 44906) figured here (Fig. 4e) as *X. yaxianensis* was originally assigned by Zhu & Lin (1978, Pl. 1, Fig 8) to *X. orientalis*. However, the discovery of the partially complete specimen figured as Fig. 4a indicates that NIGP 44906 should be reassigned.

Xystridura orientalis Zhu & Lin, 1978
FIG. 5a-g; FIG. 6a,b,f.

Xystridura orientalis Zhu & Lin, 1978 p. 441, Pl. 1, Fig. 7; Pl. 2, Figs 1-3.

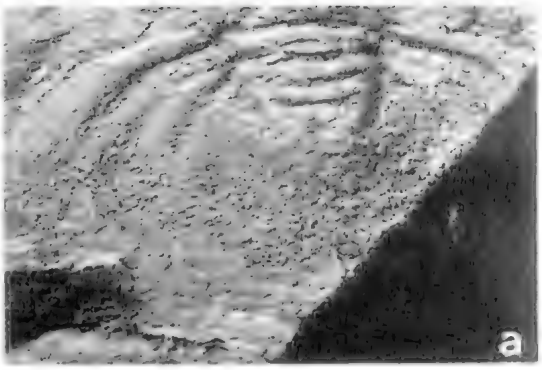
Material: One incomplete cranidium with three incomplete thoracic segments, 15 incomplete cranidia, four free cheeks and 12 incomplete pygidia.

Holotype: The cranidium (NIGP 44905) figured by Zhu & Lin 1978 (Pl. 1, Fig. 7) and refigured here as Fig. 5g.

Diagnosis: Species of *Xystridura* in which glabella extends almost to anterior border. Sharply rounded glabellar anterior. Short pygidial axis comprising three axial rings plus terminus. Three pairs of pygidial spines; anterior pair long, wide and directed slightly laterally to slightly medially; second pair long, wide and directed very slightly medially; third pair very short; posterior pygidial margin minutely denticulate.

Description: Glabella extends almost to anterior border furrow; length about 0.9 that of cranidium. Glabella has slight waist at 1p furrows; widest just anteriorly to 3p furrows. Glabellar anterior sharply rounded. Narrow shallow axial furrow. Three pairs of lateral glabellar furrows; 1p furrows directed posteromedially; 2p furrows directed slightly posteriorly; 3p furrows essentially elongated slightly anteriorly curved pits. Shallow occipital furrow deepest abaxially. Occipital ring bears small low median node. Palpebral lobe extends from opposite anterior end of occipital ring to just anteriorly of 3p furrows. Very shallow palpebral furrows. Palpebral areas of fixigenae wide, flat; narrow at anterior. Preocular sections of facial suture diverge markedly. Postocular sections of facial suture nowhere well preserved. Wide anterior border with faint terrace

Fig. 5 *Xystridura orientalis* Zhu & Lin, 1978. a, NUESD 235, cranidium plus three anterior thoracic segments, internal mould, x2; b, NUESD 238, pygidium, internal mould, x4; c, NUESD 236, librigena and partial cranidium, rubber cast of external mould, x2; d, NUESD 245, pygidium, rubber cast of external mould, x2; e, NUESD, cranidium, internal mould, x4; f, NIGP 44910, librigena, internal mould, x2.5; g, NIGP 44905, holotype cranidium (originally figured by Zhu & Lin 1978, Pl. 1, Fig. 8), internal mould, x3.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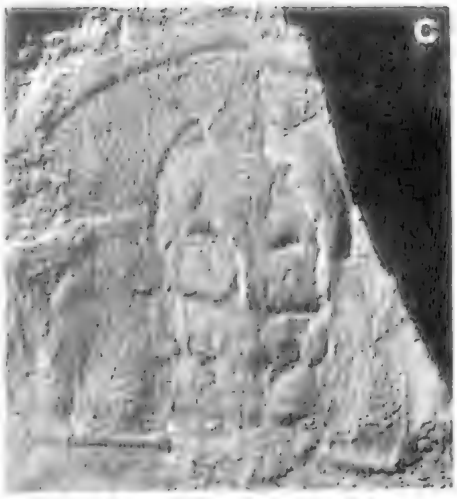
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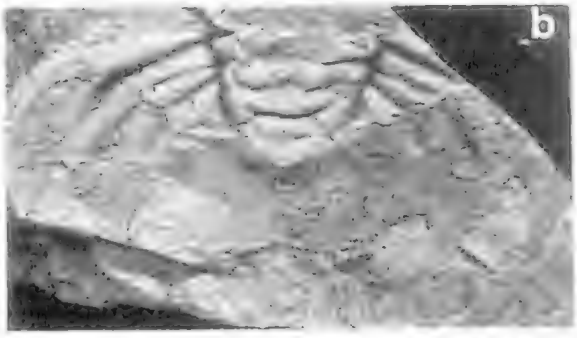
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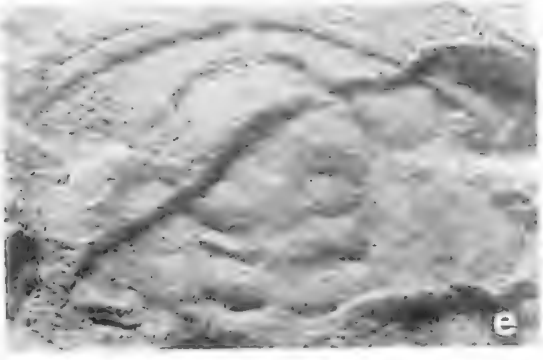
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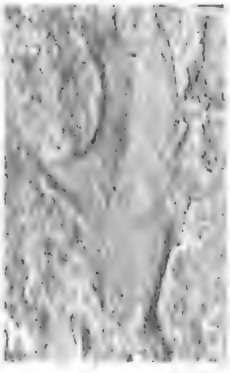

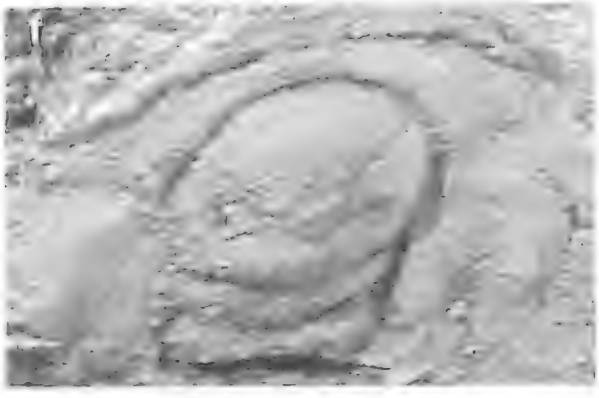
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lines; narrow anterior border furrow. Librigena has wide border with terrace lines. Border widens posteriorly; extending into long genal spine. Pygidium with three axial rings plus terminus. Axis length about 0.55 that of pygidium. Pleural field with two deep pleural furrows and two shallower interpleural furrows which extend almost all the way across very wide pleural field. Pleural field has closely spaced terrace lines. Three pairs of pygidial spines; anterior pair long, extending posteriorly and slightly outwards to slightly inwards; second pair narrower and directed very slightly medially; third pair very short; medially from the third pair pygidial margin minutely denticulate; posterior margin deflected anteriorly at centre.
Discussion: The cephalon of *X. orientalis* is essentially the same as that of *X. yaxienensis*. However, the pygidia differ in that the anterior pair of spines of *X. orientalis* are much longer than and have a broader base than those of *X. yaxienensis*. The glabellar anterior of *X. orientalis* is more sharply rounded than that of *X. hainanensis*. The anterior pair of spines on the pygidium of *X. hainanensis* is much longer than those of *X. orientalis*.

Genus GALAHETES Öpik, 1975

Type Species: Galahetes fulcrosus Öpik, 1975, p. 75, Pl. 16, Figs 1-4; Pl. 17; Pl. 18, Figs 1-3; Pl. 19, Figs 1-5; Pl. 20, Figs 1,2; text-figs 7c, 13.
Diagnosis: See Öpik 1975, p. 75.

Galahetes hainanensis Zhu & Lin, 1978
FIG. 6c,e,f,g.

Galahetes hainanensis Zhu & Lin, 1978, p. 441, Pl. 2, Fig. 4.
Galahetes pyrus Zhu & Lin, 1978, p. 442, Pl. 2, Figs 5-7.
Material: Ten cranidia.
Holotype: The cranidium (NIGP 44912) figured by Zhu & Lin 1978, Pl. 2, Fig. 4 and refigured here in Fig. 6c.
Discussion: The available specimens add nothing to the material figured in Zhu & Lin (1978). However, a re-examination of the material indicates that the cranidia described by Zhu & Lin as *Galahetes pyrus* should be placed in the same species as that described as *G. hainanensis* and hence *G. pyrus* is a junior synonym of *G. hainanensis*. The apparent differences between *G. hainanensis* and *G. pyrus* are due to the effects of tectonic distortion. The holotype cranidium of *G. hainanensis* has been tectonically elongated while the cranidium figured as *G. pyrus* by Zhu & Lin has been tectonically shortened.

Order CORYNEXOCHIDA Kobayashi, 1935
Family DORYPYGIDAE Kobayashi, 1935
Genus KOOTENIA Walcott, 1889

Type Species: Bathyuriscus (Kootenia) dawsoni Walcott, 1889, p. 446.
Diagnosis: See Palmer 1968, p. 47; 1972, p. 18.

Kootenia sp.
FIG. 2g-i, 4f.

Kootenia sp. Zhu & Lin, 1978 p. 442, Pl. 2, Figs 8,9.
Material: Two incomplete cranidia and six incomplete pygidia.
Remarks: The available material includes two pygidia which are better preserved than that figured in Zhu & Lin (1978, Pl. 2, Fig. 9). The pygidial axis comprises five axial rings and a terminus. The axis extends to the wide posterior border furrow. Narrow border. There appear to be at least five pairs of small border spines. There are four pairs of pleural furrows.

Acknowledgments

The authors wish to thank Dr Yu Zi-yi (Nanjing Institute of Geology and Palaeontology, Academia Sinica) for collecting some of the specimens. Mr Hu Shang-qing (Nanjing Institute of Geology and Palaeontology) and Mr Xu Fu-lin (Nanjing University) took the photographs. Bao Jin-song and Sun Xiao-wen provided valuable assistance in Adelaide. The University of South Australia provided financial support for Lin Tian-Rui during his visit to Australia.

Fig. 6 a,b,h *Xystridura orientalis* Zhu & Lin 1978. a, NUESD 242, pygidium, x3; b, NUESD 241, pygidium, internal mould, x3; h, NUESD 250, librigena, rubber cast of external mould, x2.
c,e,f,g. *Galahetes hainanensis* Zhu & Lin, 1978. c, NIGP 44912, holotype cranidium of external mould, (originally figured in Zhu and Lin 1978, Pl. 2, Fig. 4), x3; e, NIGP 44914, cranidium (originally figured in Zhu & Lin 1978, Pl. 2, Fig. 6 as *Galahetes pyrus*), x5; f, NUESD 215, cranidium, internal mould, x5; g, NIGP 44915, cranidium, rubber cast of external mould (originally figured in Zhu & Lin 1978, Pl. 2, Fig. 7 as *Galahetes pyrus*), x3.
d, *Pagetia luoyacunensis* sp. nov., NUESD 208, pygidium, internal mould, x20.

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EDIACARAN CARBON ISOTOPE STRATIGRAPHY OF SOUTH AUSTRALIA - AN INITIAL STUDY

BY S. D. PELL†, D. M. MCKIRDY*, J. JANSYN & R. J. F. JENKINS**

Summary

Carbon isotopic data are presented for syndepositional marine carbonates in Ediacaran (late Neoproterozoic) sedimentary sequences from the eastern Officer Basin and northern Adelaide Fold Belt, South Australia. The sediments selected for whole-rock isotopic analysis contain in excess of 10% carbonate (mostly as calcite) and very little organic matter. Recently proposed lithostratigraphic and biostratigraphic correlations allow the construction of a composite ^{13}C-curve which documents a pattern of pronounced secular variation in the isotopic signature of a terminal Proterozoic epicontinental sea (c. 590-545 Ma). Such isotopic data may reflect profound environmental changes immediately prior to the Precambrian-Cambrian transition and currently are being evaluated as a basis for worldwide chemostratigraphic correlation of sediments of this age.

KEY WORDS: carbon isotope stratigraphy, marine carbonates, kerogen, chemostratigraphic correlation, Ediacaran, Officer Basin, Adelaide Fold Belt, Rodda Beds, Wonoka Formation, Billy Springs Formation

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Summary

PELL, S. D., MCKIRDY, D. M., JANSYN, J. & JENKINS, R. J. F., (1993) Ediacaran carbon isotope stratigraphy of South Australia — an initial study. *Trans. R. Soc. S. Aust.* 117(4), 153-161, 30 November, 1993.

Carbon isotopic data are presented for syndepositional marine carbonates in Ediacaran (late Neoproterozoic) sedimentary sequences from the eastern Officer Basin and northern Adelaide Fold Belt, South Australia. The sediments selected for whole-rock isotopic analysis contain in excess of 10% carbonate (mostly as calcite) and very little organic matter. Recently proposed lithostratigraphic and biostratigraphic correlations allow the construction of a composite $\delta^{13}C$-curve which documents a pattern of pronounced secular variation in the isotopic signature of a terminal Proterozoic epicontinental sea (c. 590-545 Ma). Such isotopic data may reflect profound environmental changes immediately prior to the Precambrian-Cambrian transition and currently are being evaluated as a basis for worldwide chemostratigraphic correlation of sediments of this age.

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Introduction

Notwithstanding their perceived scarcity of fossil remains, sedimentary rocks of Neoproterozoic age hold important clues to the foundations of the present biosphere and, in particular, the origins of megascopic life (Glaessner 1984; Jenkins 1991, 1992, 1993; Knoll 1991; Knoll & Walter 1992). Worldwide multidisiplinary studies in stratigraphy, palaeontology, biogeochemistry and tectonics are now providing tantalising glimpses of the size of the crustal organic carbon reservoir during an interval of enhanced global rifting and orogeny (Des Marais *et al.* 1992) and times of massive burial of organic matter in sediments flooring stagnant, stratified oceans (Donnelly *et al.* 1990). Sea levels fluctuated and thermohaline circulation was restored during two or more ice ages (Jenkins 1991; Knoll 1991) involving low-latitude glaciation (Schmidt *et al.* 1991). Increasingly oxygenated surface waters (Knoll 1991; Derry *et al.* 1992) may be linked to the flourishing of giant microplankters (Zang & Walter 1989, 1992; Jenkins *et al.* 1992) which were a food source for the first, bizarre metazoans (Jenkins 1992). The present study focusses on two thick, well preserved but widely separated Ediacaran (late Neoproterozoic) sedimentary successions in South Australia (Fig. 1). One succession, located in the eastern Officer Basin, is largely subsurface but has been penetrated by some sixteen stratigraphic and petroleum exploration wells from which core material is available. Another is well exposed in the Flinders Ranges, part of the northern Adelaide Fold Belt[1]. The latter area is the site of the nominated Ediacaran stratotype (Jenkins 1981).

The depositional histories of the Flinders Ranges and eastern Officer Basin during Ediacaran time display striking parallels. Northward thickening prisms of sediment accumulated in both areas (Fig. 2), with southerly or centrally located shelfal regions or syndepositional flexure zones trending more or less east-west, and more rapidly subsiding troughs positioned to the north (Preiss 1987; Haines 1990; Thomas 1990; Sukanta *et al.* 1991; Preiss & Kreig 1992).

In the Flinders Ranges the several kilometres of sediment present in the southern and central shelfal regions comprise, in upward succession, the Wonoka Formation, Bonney Sandstone and Rawnsley Quartzite (Preiss 1987; Jenkins *et al.* 1992). Low in the Rawnsley Quartzite, siltstones and thin sandstones of its Ediacara Member contain the well-known Ediacara fossil assemblage (Jenkins *et al.* 1983; Gehling 1988). The Bonney Sandstone and Rawnsley Quartzite together make up the Pound Subgroup (Jenkins 1975). North of the east-west trending hinge zone (Figs 1 & 2) the Wonoka Formation and Pound Subgroup increase in thickness. In the far northeastern part of the Ranges a c. 2.1 km-thick succession of siltstone with interbeds of silty sandstone and carbonate, collectively included in the Billy Springs Formation (Preiss 1987), occupies a stratigraphic position above older parts of the Wonoka Formation and below a recently recognised condensed section of the Pound Subgroup (Reid 1992[2]). We

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[1] We favour the designation Adelaide Fold Belt (e.g. Jenkins 1990) in preference to the older usage of 'Adelaide Geosyncline' because the genetic significance of the term 'geosyncline' is unclear with respect to the ensialic characteristics of the region of outcrop.

[2] Reid, P. (1992) Ediacaran (Latest Proterozoic) stratigraphic, isotopic and palaeobiological studies in the Flinders Ranges. B.Sc. Honours thesis, University of Adelaide, unpubl.

restrict the usage of the Billy Springs Formation to exclude these upper sandstones in which rare discoidal moulds, probably representing metazoan remains, and a single fossil burrow have been observed. The Ediacaran sediments form several depositional system tracts (von der Borch *et al.* 1988; Christie-Blick *et al.* 1990; DiBona *et al.* 1990). The suggestion of glacigenic sediments within the lower member of the Billy Springs Formation (DiBona 1991) has not been substantiated by the reporting of diagnostic characteristics such as facetted and striated clasts or till pellets.

The Flinders Ranges underwent local extensional faulting during early Wonoka Formation time. The subsequent Cambro-Ordovician Delamerian Orogeny (Preiss 1987) shortened the sedimentary pile at several thrust zones and formed open to tight folds.

In the eastern Officer Basin, the Rodda Beds (Brewer *et al.* 1987) include thin carbonates resembling the Wonoka Formation that extend across its southern shelfal region (Murnaroo Platform; Thomas 1990; Sukanta *et al.* 1991). These carbonates lie above correlatives of the Bunyeroo Formation which include an important chronostratigraphic marker, the Acraman impact ejecta horizon (Wallace *et al.* 1989), formed by the debris of a giant meteorite infall. The Wonoka-like carbonates of the Rodda Beds are host to large leiosphaerids and process-bearing acritarchs, potentially of regional biostratigraphic significance (Jenkins *et al.* 1992). Extensional faulting again characterises the start of the Ediacaran cycle which, in this instance, is signalled by seismic reflector F_5 (Thomas 1990; Sukanta *et al.* 1991). Farther north, in the Munyarai Trough (Fig. 1), presumed equivalents of the Wonoka Formation are represented by a prism of sediments as much as several kilometres thick. Reflector F is an erosively downcutting surface and marks the incision of large, canyon-like structures (Thomas 1990; Sukanta *et al.* 1991) with basal pebbly beds and infilling siltstones that resemble the Billy Springs Formation. Subsequent reflectors or sequence boundaries are speculatively equated with erosive events recorded in the Pound Subgroup, and the base of the Cambrian is a regional disconformity, surface E (Thomas 1990; Sukanta *et al.* 1991).

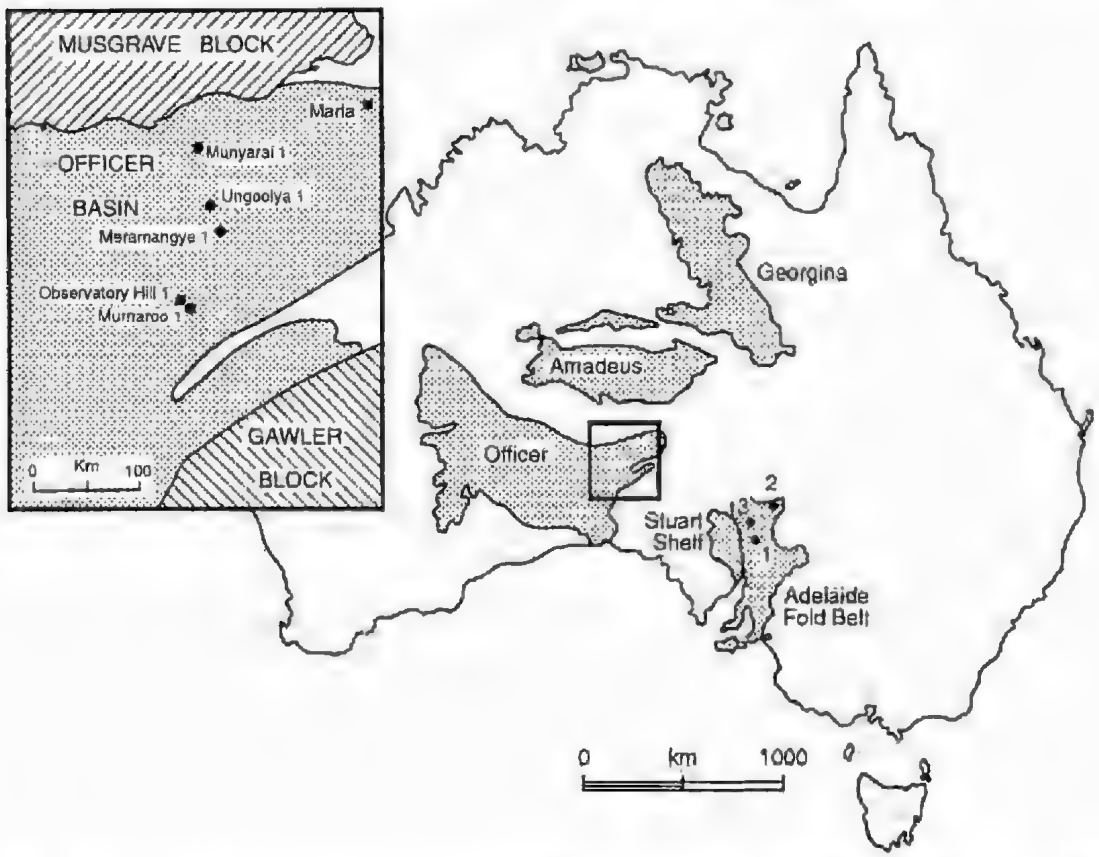

Fig. 1. Map of Officer Basin, Adelaide Fold Belt and other central Australian basins containing thick sequences of Ediacaran (late Neoproterozoic) sedimentary rocks. Inset shows location of drillhole intersections in the Officer Basin. Specific outcrop localities: 1, Bunyeroo Gorge (site of Ediacaran type section); 2, Mount Freeling Syncline; 3, Black Range Springs.

Materials and Methods

A generalised synthesis of these stratigraphies (Fig. 2) provides the regional framework within which we place our carbon isotopic measurements ($\delta^{13}C_{PDB}$ of whole-rock carbonate: Kaufman *et al.* 1991) made on cores from four drillholes in the Officer Basin and on outcrop specimens from surface sections in the central and northeastern Flinders Ranges (Fig. 3). The samples selected for isotopic analysis are fine-grained sedimentary rocks containing 1.2-12% carbonate carbon (CC; equivalent to 10-100% $CaCO_3$). Their carbonate mineralogy as determined by XRD analysis is mixed (calcite, dolomite), although calcite is the dominant component in more than 75% of the samples examined. Carbon isotopic composition in contiguous strata appears to be independent of mineralogy, suggesting that dolomitisation was early and took place in a closed diagenetic system. Total organic carbon (TOC) contents of the dolomicrites and calcareous and dolomitic siltstones from the Officer Basin are negligible to moderate (0.03-0.87%) and the dispersed organic matter is of relatively low thermal maturity (kerogen atomic H/C = 0.80-1.15; Rock-Eval T_{max} = 419-443°C: McKirdy *et al.* 1992). Weak metamorphism in the central Flinders Ranges (Lemon *et al.* 1992) increases to greenschist facies (biotite zone) in the northeastern region (McKirdy *et al.* 1975; Preiss 1987). Fine-grained lithofacies in both the Wonoka Formation and Billy Springs Formation are organically very lean (TOC mostly ≤0.1%). In the Mount Freeling Syncline there is some evidence of metamorphic loss of organic carbon from these units.

Results and Discussion

The oldest Ediacaran sediments in South Australia, offshore arenites and siltstones and a storm-dominated succession of ramp carbonates deposited below fairweather wave base, are represented by the lower to mid-Wonoka Formation in Bunyeroo Gorge (Haines 1990). Shallow-water (lagoonal to supratidal) carbonates of the upper Wonoka Formation were sampled here and at two other localities in the central and northern Flinders Ranges (Fig. 3). The resulting composite carbon isotope stratigraphy (Fig. 4) displays the following features: a low negative value ($\delta^{13}C$ = -2.4‰) in the basal dolomicrite horizon (Unit 1); a shift to strongly negative $\delta^{13}C$ values (-6 to -8.5‰) which persist through 360 m of outer to middle shelf limestones (Units 3-7); and a steady positive trend from midway through Unit 7 (-6‰) into Unit 9 (+4.5‰),

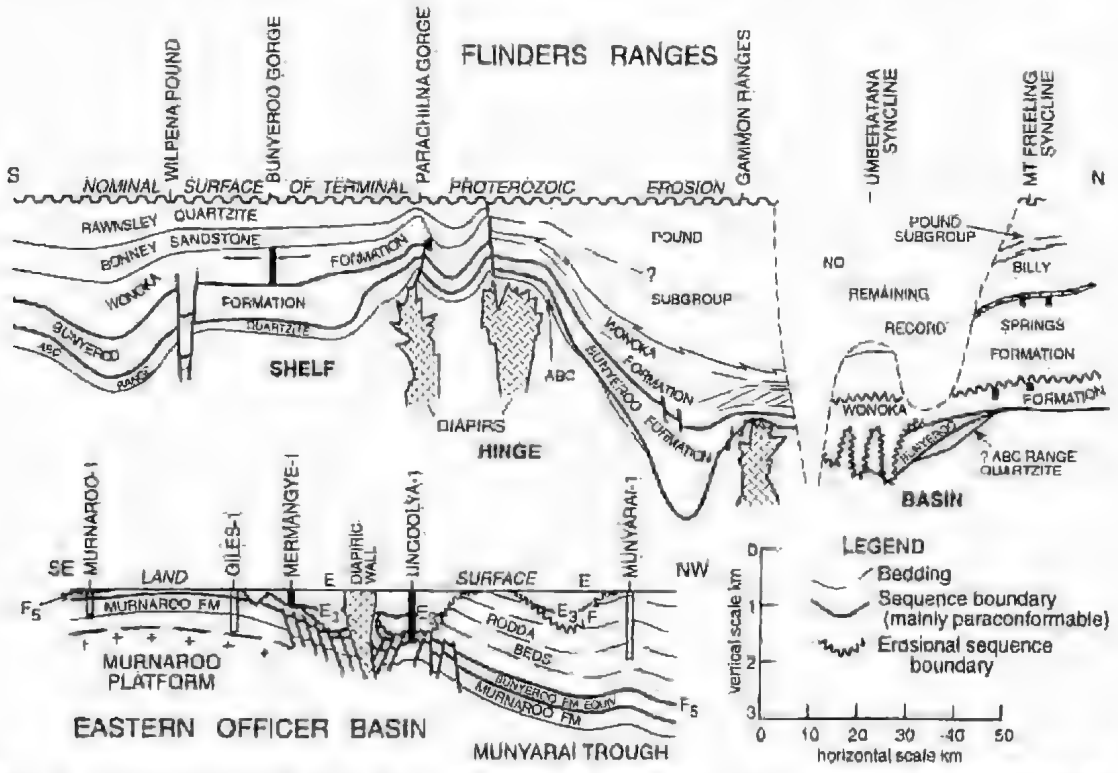

Fig. 2 Comparison of generalised seismic section of the later Neoproterozoic of the eastern Officer Basin (based on the interpretations of Thomas 1990 and Sukanta *et al.* 1991) and the correlative stratigraphy of the Flinders Ranges.

Moderately positive $\delta^{13}C$ values (+4 to +6‰) are maintained through the Wonoka-like carbonates in the Officer Basin at Murnaroo-1 and Observatory Hill-1 (Fig. 3). This interval includes giant process-bearing acritarchs in the Officer Basin (Jenkins *et al.* 1992). Probable early indications of metazoans in the Flinders Ranges occur in Unit 10 of the Wonoka Formation (Jenkins 1984, 1993; Haines 1990). Sequence stratigraphic data from the northern Gammon Ranges (DiBona *et al.* 1990) suggest that Unit 10 predates the Billy Springs Formation.

Our next segment of the Ediacaran carbon isotope profile comes from the eastern Mount Freeling Syncline where carbonates at the top of the lower member of the Billy Springs Formation are exposed (Fig. 3). Here the record is fragmentary and incomplete, largely because of structural complexity and the scarcity of suitable carbonate lithologies. Nevertheless, the available data appear to delineate a second major positive excursion; $\delta^{13}C$ values rise from -0.7 to +7‰ over a section of several hundred metres and (with one exception: +2.7‰) remain relatively constant through the prominently outcropping carbonate that forms the ridge of Wildman Bluff. We consider that the uppermost Wonoka Formation (Unit 11) may be coeval with some part of the Billy Springs Formation. Unit 11 at Black Range Springs ($\delta^{13}C$ = +6.6‰: Urlwin 1992[3]) also records a positive isotopic excursion. The more muted expression of this excursion in the same unit at Bunyeroo Gorge ($\delta^{13}C$ = +2‰: Fig. 3) may reflect increased oxidation and recycling of ^{13}C-depleted organic matter in restricted, shallow, lagoonal environments which contrast with the presumed open-marine conditions farther north (Haines 1990).

[3] Urlwin, B. (1992) Carbon isotope stratigraphy of the late Proterozoic Wonoka Formation of the Adelaide Fold Belt: diagenetic assessment and interpretation of isotopic signature, and correlations with previously measured isotopic curves. B.Sc. Honours thesis, University of Adelaide, unpubl.

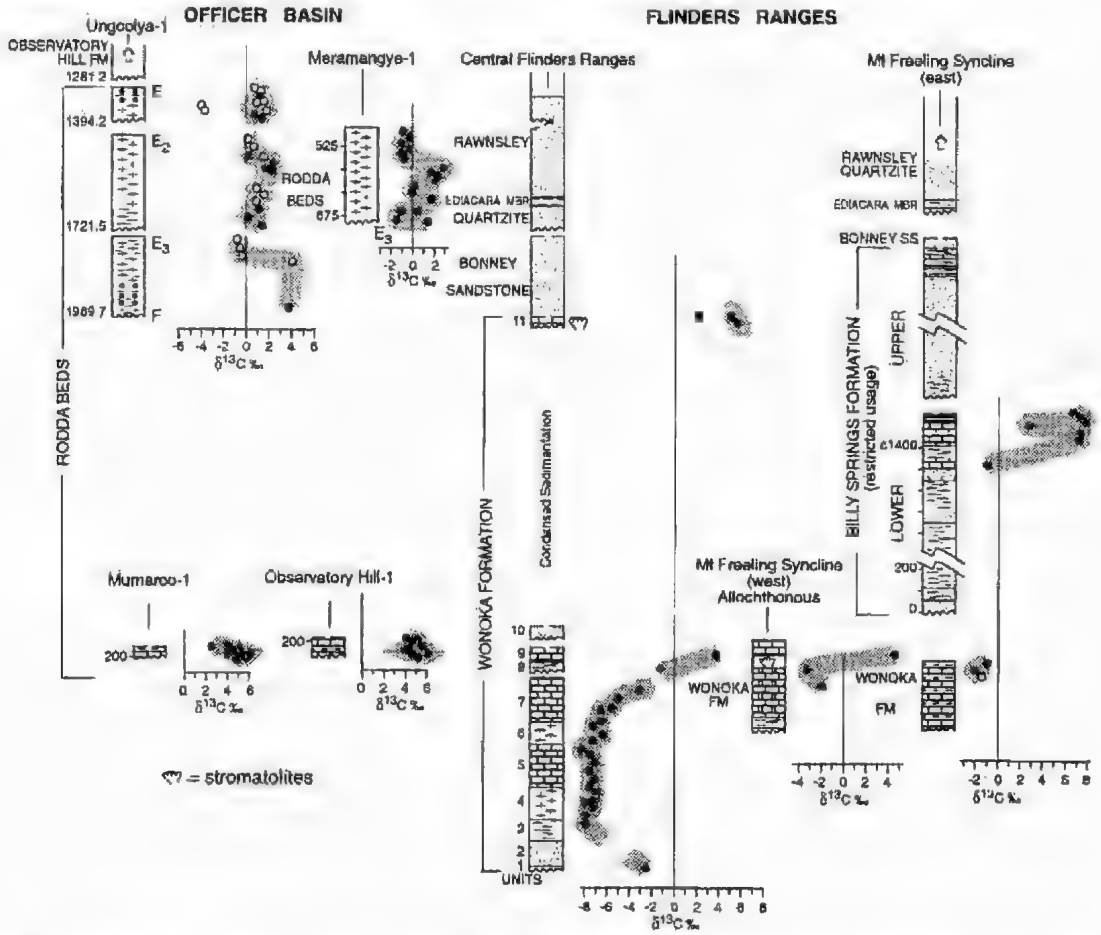

Fig. 3. Carbon isotope profiles of carbonate-bearing Ediacaran sequences in four drillholes from the eastern Officer Basin and three surface sections from the Flinders Ranges. Key: o 1-2% carbonate carbon; • >2% carbonate carbon.

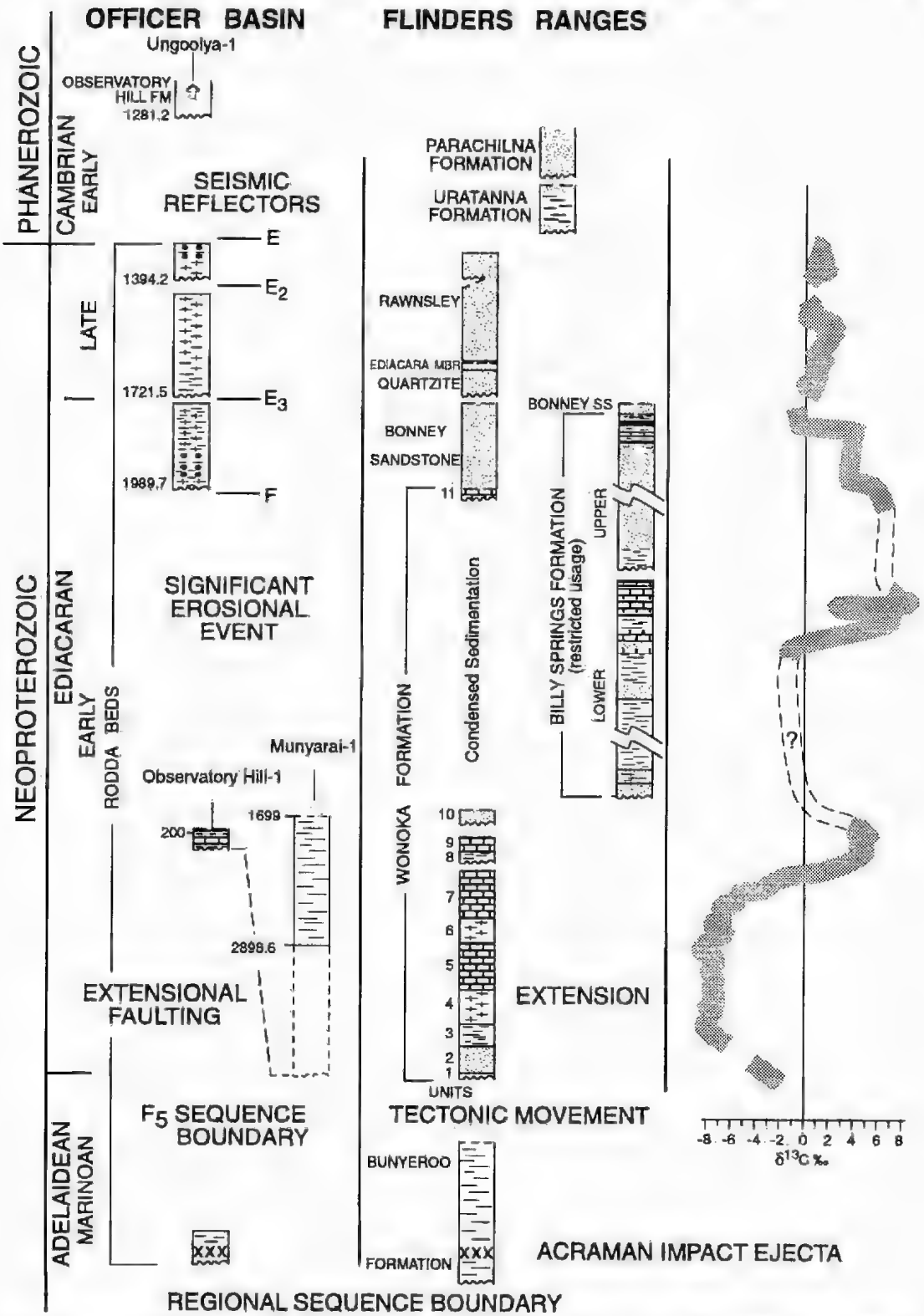

Fig. 4. Summary of Ediacaran carbon isotope stratigraphy of the Officer Basin and Flinders Ranges, South Australia.

In the central Flinders Ranges, sediments of mid and late Ediacaran age (Bonney Sandstone and Rawnsley Quartzite) are devoid of carbonate. Fortunately, in the eastern Officer Basin suggested correlatives in the upper Rodda Beds (Sukanta *et al.* 1991; Jenkins *et al.* 1992) include calcareous and dolomitic siltstones (Pell 1989[4]). Their detailed carbon isotope stratigraphy at Ungoolya-1 and Meramangye-1 is displayed in Fig. 3. Sediments from the 1720-1990 m depth interval of Ungoolya-1 are for the most part carbonate-poor (CC = 0.5-7.1%). The $\delta^{13}C$ values of such carbonate (mostly in the range -0.8 to +0.2 ‰) must be interpreted with caution (Lambert *et al.* 1987; Fairchild *et al.* 1990). Kerogens isolated from the lower half of the succession provide a very coherent $\delta^{13}C$ signal (-25 to -26 ‰). Moreover, the mean difference between the $\delta^{13}C$ values of carbonate and organic carbon in these sediments ($\Delta^{13}C \approx 25$ ‰) coincides with the second of two modes in the frequency distribution of $\Delta^{13}C$ values for carbonate-rich Rodda Beds (discussed below). We therefore suggest that the two lone positive $\delta^{13}C$ values at 1964.6 m and 1809.5 m in Ungoolya-1 (+3.8 ‰ and +4.2 ‰; Fig. 3) do actually record the isotopic composition of primary marine carbonate deposited at this mid Ediacaran highstand tract (Jenkins *et al.* 1992), and that shifts to more negative values (in the range +0.2 to -0.8 ‰) represent diagenetic carbonate resulting from bacterial oxidation of organic matter. These slightly calcareous and dolomitic siltstones are not notably pyritic, precluding bacterial sulphate reduction as a significant additional source of biogenic CO_2.

Equivalent late Rodda Beds sections at Ungoolya-1 and Meramangye-1 exhibit similar carbonate $\delta^{13}C$ trends (Fig. 3). In each instance many of the samples analysed are reasonably carbonate-rich (CC > 2%) and therefore likely to retain primary marine isotopic signatures. A sharp negative excursion from +1 to -1.5 ‰ at the base of the Rodda Beds penetrated by Meramangye-1 appears to record detail not documented by our sampling of the equivalent interval immediately above the E_3 seismic reflector in Ungoolya-1 (Fig. 3). The ensuing steady return to positive $\delta^{13}C$ values (peaking at +2.7 and +1.9 ‰, respectively) in both well sections is followed by a second negative excursion, although erosive loss of section attenuates this trend at Ungoolya-1. Carbonate in the highest part of the Rodda Beds section at Ungoolya-1 is for the most part characterised by moderately positive $\delta^{13}C$ values (+0.9 to +1.7 ‰; Fig. 3). Two anomalously negative values (-3.8 and -3.6 ‰) again are associated with strata in which carbonate contents are relatively low and hence may not be wholly of primary origin.

The extent to which primary marine carbon isotopic compositions have been retained throughout the Rodda Beds is difficult to ascertain. One strategy adopted by previous workers to overcome the problem of diagenetic alteration involves $\delta^{13}C$ measurement on carbonate and organic carbon in the same sample (Knoll *et al.* 1986). Primary processes (notably synthesis of organic matter by marine autotrophs and precipitation of carbonate in equilibrium with CO_2 dissolved in the water column) tend to maintain a constant isotopic difference between carbonate and organic carbon, whereas various secondary processes may independently alter $\delta^{13}C$ in either carbon phase (McKirdy & Powell 1974; Irwin *et al.* 1977; Hayes *et al.* 1983). Thermal maturation of the Rodda Beds has not been severe enough to significantly modify the primary isotopic composition of their kerogen. Even so, for the carbonate-rich strata examined, $\Delta^{13}C$ ranges from -24 ‰ to -36 ‰; and the frequency distribution of these $\Delta^{13}C$ values is distinctly bimodal (Fig. 5). It is likely that the dominant mode at 34 ‰ represents the primary isotopic separation between coexisting Ediacaran organic and inorganic carbon in the Officer Basin. This contrasts with the reported modal $\Delta^{13}C$ value of 28.5 ‰ for Upper Riphean and incomplete Vendian sections in Svalbard and East Greenland (Knoll *et al.* 1986). One recognised cause of enhanced isotopic fractionation between carbonate and organic carbon is methanogenic diagenesis (Irwin *et al.* 1977). An alternative explanation is suggested by the results of recent studies which have revealed that Neoproterozoic marine sediments containing well-preserved kerogens exhibit wide secular fluctuations in $\Delta^{13}C$ (Strauss *et al.* 1992; Des Marais *et al.* 1992). In particular, the degree of fractionation between coexisting carbonate and organic carbon recorded in such sediments increases significantly between 900 and 600 Ma ago, at a time when the atmospheric CO_2/O_2 ratio was in decline prior to the Varanger glaciation. Our $\Delta^{13}C$ data are in excellent agreement with the terminal Proterozoic (~600 Ma) separation of $\delta^{13}C_{carb}$ and $\delta^{13}C_{org}$ reported by Des Marais *et al.* (1992, figs 1 & 2). Presumably there was near optimum isotopic fractionation during photosynthetic fixation of dissolved carbon dioxide in the Ediacaran seaway of the Officer Basin (cf. Strauss *et al.* 1992).

The $\Delta^{13}C$ distribution for Ediacaran (Rodda Beds) carbonate – organic carbon pairs has a secondary mode at 25 ‰ (Fig. 5). This manifestation of a low fractionation of the C isotopes tends to be associated with negative carbonate $\delta^{13}C$ values, and hence probably reflects appreciable diagenetic precipitation of carbonate in response to *in situ* bacterial oxidation of organic material with an isotopic composition ($\delta^{13}C$

[4] Pell, S. D. (1989) Stable isotope composition of organic matter and co-existing carbonate in the Late Precambrian of the Officer Basin: stratigraphic relationships with neighbouring basins and environmental significance. B.Sc. Honours thesis, University of Adelaide, unpubl.

= -23 to -28‰) typical of planktic organic carbon from ocean waters with surface temperatures in the range of 0-10°C (Sackett *et al.* 1974). It is CO_2 (or bicarbonate) availability, not temperature *per se*, which ultimately controls the extent of discrimination against ^{13}C during photosynthetic carbon fixation (Anderson & Arthur 1983). This in turn is a function of several variables, including pCO_2 in the external environment (Arthur *et al.* 1985); the development and operation of biochemical pumps for bicarbonate and carbon dioxide (Badger 1987); and evolutionary changes to the kinetic properties of the principal CO_2-fixing enzyme in prokaryotic and eukaryotic photoautotrophs (Badger & Andrews 1987). All these factors were in a state of considerable flux during the Neoproterozoic (Strauss *et al.* 1992) which witnessed *inter alia* the emergence and decline of giant phytoplankters (Zang & Walter 1989; Jenkins *et al.* 1992; Knoll & Walter 1992). Hence, it is perhaps not surprising that contrasting microfossil assemblages (one dominated by spinose acritarchs and the other by filamentous forms) from widely separate stratigraphic levels of the Rodda Beds (Jenkins *et al.* 1992) should display markedly different $\delta^{13}C$ organic signatures (-29 to -31‰ and -25 to -26‰, respectively).

Conclusions

Our composite carbon isotope trend (Fig. 4) shows that for several periods of its history the Ediacaran seaway in South Australia was precipitating isotopically heavy primary carbonate ($\delta^{13}C$ = +0.5 to +6‰). Similar ^{13}C-enriched carbonates have been documented in other Neoproterozoic successions (e.g. Knoll *et al.* 1986; Aharon *et al.* 1987; Lambert *et al.* 1987; Brasier *et al.* 1990; Fairchild *et al.* 1990; Kaufman *et al.* 1991; Magaritz *et al.* 1991) and attributed to the maintenance of abnormally high rates of burial of organic matter in shallow epicontinental seas at low palaeolatitudes (Donnelly *et al.* 1990; Derry *et al.* 1992). Conversely, the prominent negative excursion recorded in the Wonoka Formation may reflect recycling of organic matter from planktic and benthic primary producers (Jenkins *et al.* 1992) by (?)metazoan grazers and aerobic bacteria inhabiting the oxic water column of a storm-prone, deep water, ramp environment. Ongoing studies of this lithological unit at localities up to 200 km apart suggest that the markedly negative $\delta^{13}C$ values (-6 to -8‰) which characterise much of the older Wonoka Formation are a basinwide phenomenon (Urlwin *et al.* 1993); and we draw attention to the unexceptional isotopic signals recorded from Unit 1 and through Units 7, 8 and 9. A careful trace element and isotopic study by Ayliffe (1992[5]) demonstrated that part of the Wonoka Formation filling a deep 'submarine' canyon (>700 m of erosional relief) and displaying the same regional low $\delta^{13}C$ signal (Urlwin *et al.* 1993; Fig. 1) has never been in contact with meteoric waters. Morever, the 'pristine' (low) strontium isotope ratio of the canyon fill is strong evidence that there has been negligible alteration by epigenetic fluids. Sedimentological characteristics of the older Wonoka Formation are consistent with the precipitation of its calcium carbonate as whitings (Haines 1990), perhaps implying a low pCO_2 in the surface waters of the ambient sea.

[5] Ayliffe, D. J. (1992) Geological setting of the Late Proterozoic Wonoka Formation at Pichi Richi Pass, southern Flinders Ranges: geochemical, stable isotope and diagenetic analysis. B.Sc. Honours thesis, University of Adelaide, unpubl.

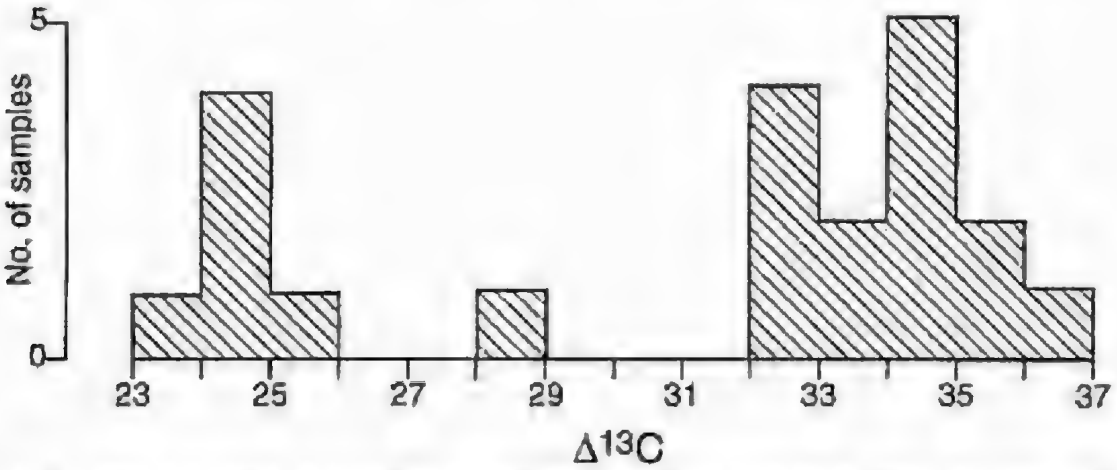

Fig. 5. Frequency distribution of $\Delta^{13}C$ values in carbonate-rich strata of the Rodda Beds, eastern Officer Basin. Note: $\Delta^{13}C = \delta^{13}C_{carb} - \delta^{13}C_{org}$ (after Knoll *et al.* 1986).

The uniformly sparse TOC content of these sediments also is consistent with a lowered primary productivity, and hence it is conceivable that their carbon isotope signature flags the development of a 'Strangelove ocean' (see Hsu *et al.* 1985) in which biological productivity is totally poisoned by abnormally high concentrations of dissolved O_2 (e.g. Jenkins 1991). Derry *et al.* (1992) concluded that, at about this time, the biosphere first entered its oxygenic Phanerozoic mode following a large and rapid flux of O_2 out of the carbon cycle.

The younger part of our Ediacaran $\delta^{13}C$ profile (Fig. 4) broadly parallels the isotope curve published by Lambert *et al.* (1987) for the late Neoproterozoic carbonate-rich Doushantou and Dengying Formations of the Yangtze Platform, China. In both instances, isotopically heavy carbonate ($\delta^{13}C$ = +4 to +7‰) is followed by a trend towards lighter although still mostly positive $\delta^{13}C$ values (+0.5 to +3‰) in overlying strata. In this respect, the $\delta^{13}C$ trends summarised in Fig. 4 may also be compared with data from carbonate sections of the Nama Group, Namibia (Kaufman *et al.* 1991) showing one marked positive excursion (from −6 to +6‰) in the lower part of the succession (Kuibis Formation) and relatively stable, moderately positive values (+1 to +2.5‰) through the overlying Schwarzrand Formation. There is independent evidence, based on occurrences of Ediacaran soft-bodied metazoan fossil remains (Awramik *et al.* 1985; Sun 1986; Jenkins 1992, 1993), that these three successions in South Australia, China and Namibia are broadly coeval. The largely siliciclastic Rodda Beds are generally leaner in carbonate than the corresponding Chinese and Namibian sections and hence their isotope record is more susceptible to diagenetic alteration. Nevertheless, two minor negative excursions expressed in the Late Ediacaran profile from Meramangye-1 (Fig. 3) appear to be real and not diagenetic artefacts. Their significance has yet to be evaluated, but they may prove to be useful in future inter-regional chemostratigraphic correlations (Brasier *et al.* 1990; Magaritz *et al.* 1991; Knoll & Walter 1992).

Acknowledgments

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TWO NEW SPECIES OF NEMATODE (NEMATODA: ENOPLIDA: THORACOSTOMOPSIDAE) FROM LAKE ALEXANDRINA, SOUTH AUSTRALIA

*BY W. L. NICHOLAS**

Summary

Two new species of Thoracostomopsidae (Nematoda: Enoplida) are described from Lake Alexandrina near the mouth of the River Murray in South Australia. *Mesacanthion alexandrinus* sp. nov. belongs to the small group of congeners with unequal spicules, but differs in having only slightly unequal spicules and a simple gubernaculum. *Enoploides stewarti* sp. nov. is very similar to another freshwater species, *E. fluviatilis* from the River Volga, but differs in minor details of the spicules and supplementary organ. *Enoploides* and *Mesacanthion* are typically marine genera and implications of the presence of these two new species in freshwater Lake Alexandrina are discussed.

KEY WORDS: Taxonomy, nematodes, distribution, Thoracostomopsidae, River Murray, South Australia, *Mesacanthion alexandrinus* sp. nov. *Enoploides stewarti* sp. nov.

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KEY WORDS. Taxonomy, nematodes, distribution, Thoracostomopsidae, River Murray, South Australia, *Mesacanthion alexandrinus* sp. nov; *Enoploides stewarti* sp. nov.

Introduction

The numerous species of the genera *Mesacanthion* and *Enoploides* have worldwide distributions characteristically inhabiting ocean beaches. Several species of both genera have been found in freshwater (Riemann 1975). The two new species described in this paper come from Lake Alexandrina, a large freshwater lake at the mouth of the River Murray, which has only comparatively recently (in 1940) been isolated from the sea by barrages built across the estuary. The nematode fauna of the estuary and of Lake Alexandrina has been described by Nicholas *et al.* (1992), together with observations on hydrology and sedimentology.

Thoracostomopsidae Filipjev, 1927, possess mandibles, one dorsal and two sub-ventral, terminating in recurved hooks that project into the buccal cavity. In *Mesacanthion* Filipjev, 1927, the mandible is formed from two lateral rods joined by an anterior curved bar, enclosing a roughened membrane. In *Enoploides* Ssaweljev, 1912, the lateral bars are fused for most of their length to form a solid rod, without any enclosed membrane, bifurcated anteriorly into curved hooks. In both genera a forwardly directed tooth (onchium), with the opening of the duct of a pharyngeal gland at the tip, lies at the base of each mandible. The cephalic setae are inserted further forward on the cephalic capsule in *Mesacanthion* than in *Enoploides*.

Materials and Methods

The new species were collected during the investigation of the nematode fauna of Lake Alexandrina already referred to (Nicholas *et al.* 1992), in which 490 ml samples of sandy sediment were taken with a metal corer to a depth of 5 cm at the waters edge. Further details of procedure, sampling and a map locating sampling sites are given in the paper cited. Nematodes were extracted from the sediments by differential sedimentation in tap water, collected on a nylon 75μm sieve, fixed in 5% formalin, transferred to 5% aqueous glycerol, which was evaporated to anhydrous glycerol at 37°C. After identification under the microscope, permanent mounts were made in anhydrous glycerol.

Mesacanthion alexandrinus sp. nov.
FIGS 1, A-E, 2, A-D, Table 1

Types: Holotype: male, Lake Alexandrina, South Australia, 18.vii.1989, coll. W. L. Nicholas and A. F. Bird, in SAM 23875; paratypes: 2 males and 2 females, Lake Alexandrina, South Australia, 16.vi.1989, 20.viii.1989, coll. W. L. Nicholas and A. F. Bird, in SAM 23876-79; male and female, Lake Alexandrina, South Australia, 18.vii.1989, coll. W. L. Nicholas and A. F. Bird, 18.viii.1989 in W. L. Nicholas collection, slides 1220, 1221.

Description of Holotype male. Cuticle smooth, not annulated, with sparse setae, up to 17 μm long, along the entire body, but fewer and shorter towards the posterior end. Cephalic capsule high, 2.6 times width at base, dome-shaped, with three deeply incised lips, each carrying thin triangular lip-flap. Six 12 μm long labial setae insert at base of lip-flaps. Six 29 μm inner cephalic setae and four adjacent 14 μm outer cephalic setae originate about half-way up cephalic capsule. Three broad mandibles (width ⅔ height), edged by strong lateral and transverse bars, lateral bars terminating in divergent hooks, broad inter-bar membrane externally rough; three onchia at base of

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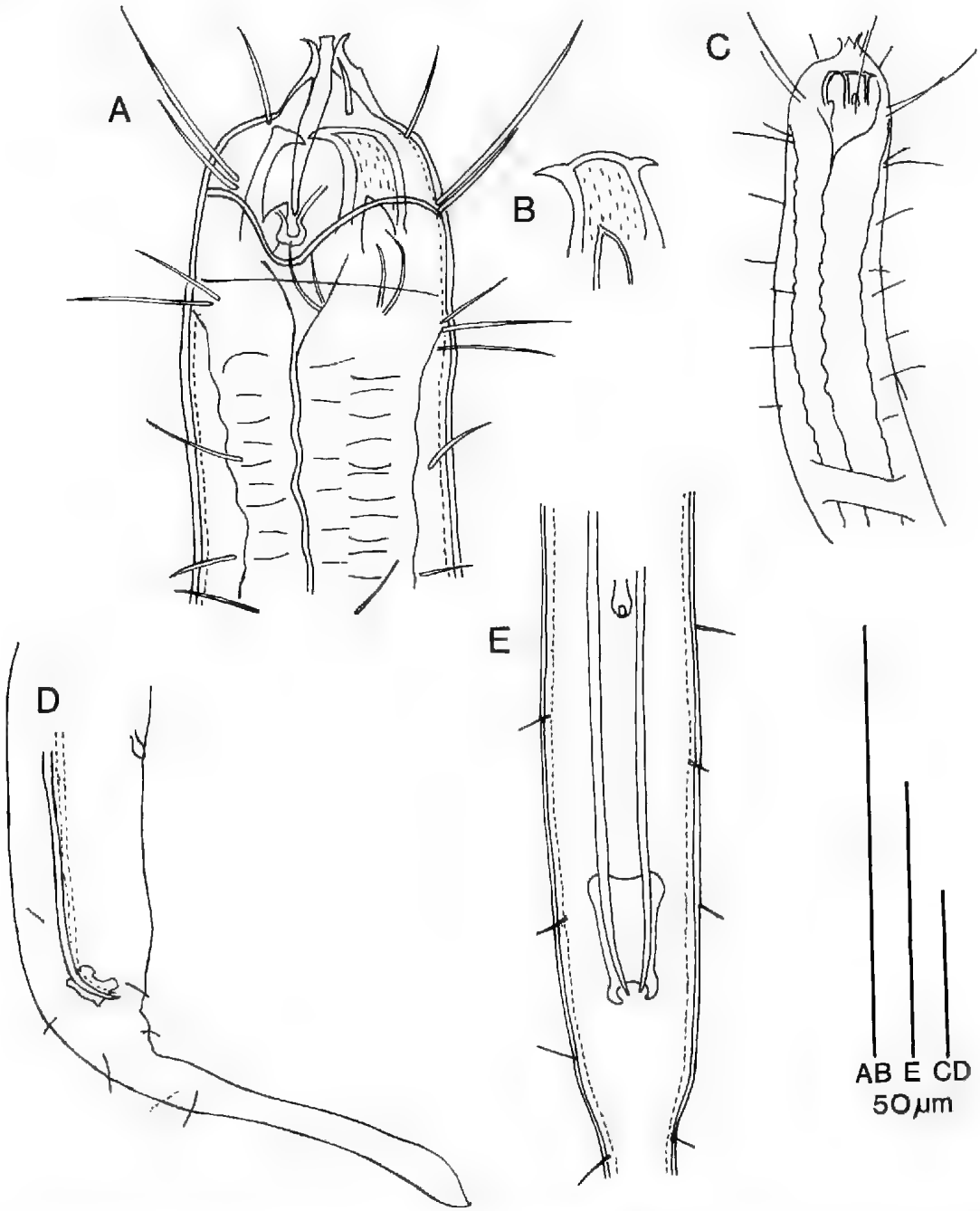

Fig. 1. Male *Mesacanthion alexandrinus* sp. nov. A, head; B, mandible and onchium; C, head and cervical region; D. spicules and supplementary organ in lateral view; E, spicules and supplementary organ in *dorsal* view.

mandibles. Six pairs of cervical setae inserted immediately posterior to cephalic capsule, each pair with anterior short (10 μm) and posterior long (17 μm) seta. Pharynx long, cylindrical; cardia conical; rectum short, 1.3 times body width at cloaca. Testes, two, opposed, to right of intestine. Two long slightly unequal spicules, with straight shaft curving ventrally towards tip. Gubernaculum flat plate with two terminal hooks, no apophysis; supplementary organ globular, inconspicuous, anterior to and 2.6 body widths from cloaca. Shorter spicule reaches level of supplement (78 μm; 3.1 body widths) longer just beyond it (86 μm, 3.4 body widths). Tail short, narrows sharply behind cloaca then cylindrical almost to tip. Additional dimensions see Table 1.

Paratypes: One male, SAM 23877, displays the spicules in dorsal view (Fig. 1 E) with right spicule longer, and gubernaculum with hooks. Females resemble males, apart from sexual organs, but lack six pairs of cervical setae and, unlike males, tail tapers uniformly to tip. Didelphic opposed gonads. Measurements in Table 1.

Habitat: Freshwater, sand at waters edge of Lake Alexandrina, South Australia.

Comparison with other species: Wieser (1953) published a key to *Mesacanthion* which he later updated (Wieser 1959). The spicules and gubernaculum provide the most useful specific characters, but because some species had been described only from females it was necessary to find characters applicable to females. The depth and form of the buccal cavity and length of the cephalic setae are also useful. Species described only from juveniles were considered *species inquirendae*. Subsequently, Gerlach & Riemann (1974) listed 40 valid species. Since then four more species have been described: *M. southerni* Warwick, 1973, *M. arabium* Warwick, 1973, *M. heterospiculum* Sergeeva, 1974, and *M. marisalba* Galtsova, 1976.

M. alexandrinus sp. nov. belongs to the small group with unequal spicules. In *M. diplechma* (Southern, 1914), redescribed by Boucher (1977) and *M. southerni*, the spicules are very unequal, whereas in *M. alexandrinus* sp. nov. they are both long and only slightly unequal. The gubernaculum in *M. arabium* is like that of *M. alexandrinus*, sp. nov, but the former is much larger, has equal spicules, and possesses two rows of stout pre-cloacal setae. *M. longispiculum* Gerlach, 1954 resembles the new species, but has much longer and equal spicules. In *M. heterospiculum* the spicules are uniformly curved, the tail is conical and uniformly tapered, the cuticle annulated.

In comparison with species described only from females, all included in Wieser (1959), *M. alexandrinus* sp. nov. belongs to the group in which the buccal cavity is deep, conical, without basal pockets. It can be distinguished from all the others, either because it has very short labial setae or possesses very long cephalic setae, or has setae arising close to the base of the cephalic capsule.

TABLE 1. *Measurements of* Mesacanthion alexandrinus. *sp. nov.*

Type	holo	para	para	para	para	para	para
Sex	Male	Male	Male	Male	Female	Female	Female
Slide	23875	23876	23877	1220	23878	23879	1221
Length	1630	1780	1450	2460	2560	2270	2570
Max. width	38	54	37	59	66	86	60
Labial setae	12	13	12	12	12	9	12
Inner cephalic	29	27	28	29	27	27	28
Outer cephalic	14	13	12	16	11	16	19
Mandible h×w	9×14	8×10	8×10	12×14	8×13	12×14	14×15
Head, h×w	22×33	22×33	20×27	28×36	26×38	15×20	21×33
Nerve ring	126	141	114	153	151	180	160
Pharynx	526	504	430	575	730	594	718
Vulva	–	–	–	–	1600	1242	1406
Tail	108	131	97	110	139	137	136
Width at anus	25	29	23	32	33	32	36
Spicules, arc	78; 86	70; 79	72;82	69;80	–	–	–
Supplement	66	70	64	69	–	–	–
Tail/anal breadth	4.32	4.52	4.22	3.44	4.21	4.28	3.44
Nerve ring/pharynx	0.24	0.28	0.27	0.26	0.21	0.30	0.22
L. ceph. setae/hw	0.42	0.39	0.44	0.40	0.31	0.42	0.50
Mandible h/w	0.64	0.80	0.80	0.85	0.62	0.85	
Spicule/anal width	3.12; 3.44	2.41; 2.72	3.13; 3.56	2.15; 2.5			
De Man's ratio a	43	33	39	42	39	26	42
" b	3.1	3.5	3.4	3.6	3.5	3.8	3.6
" c	15	14	15	22	18	17	19
" c'	4.3	4.5	4.2	3.4	4.2	4.3	3.8
" V%					63	55	55

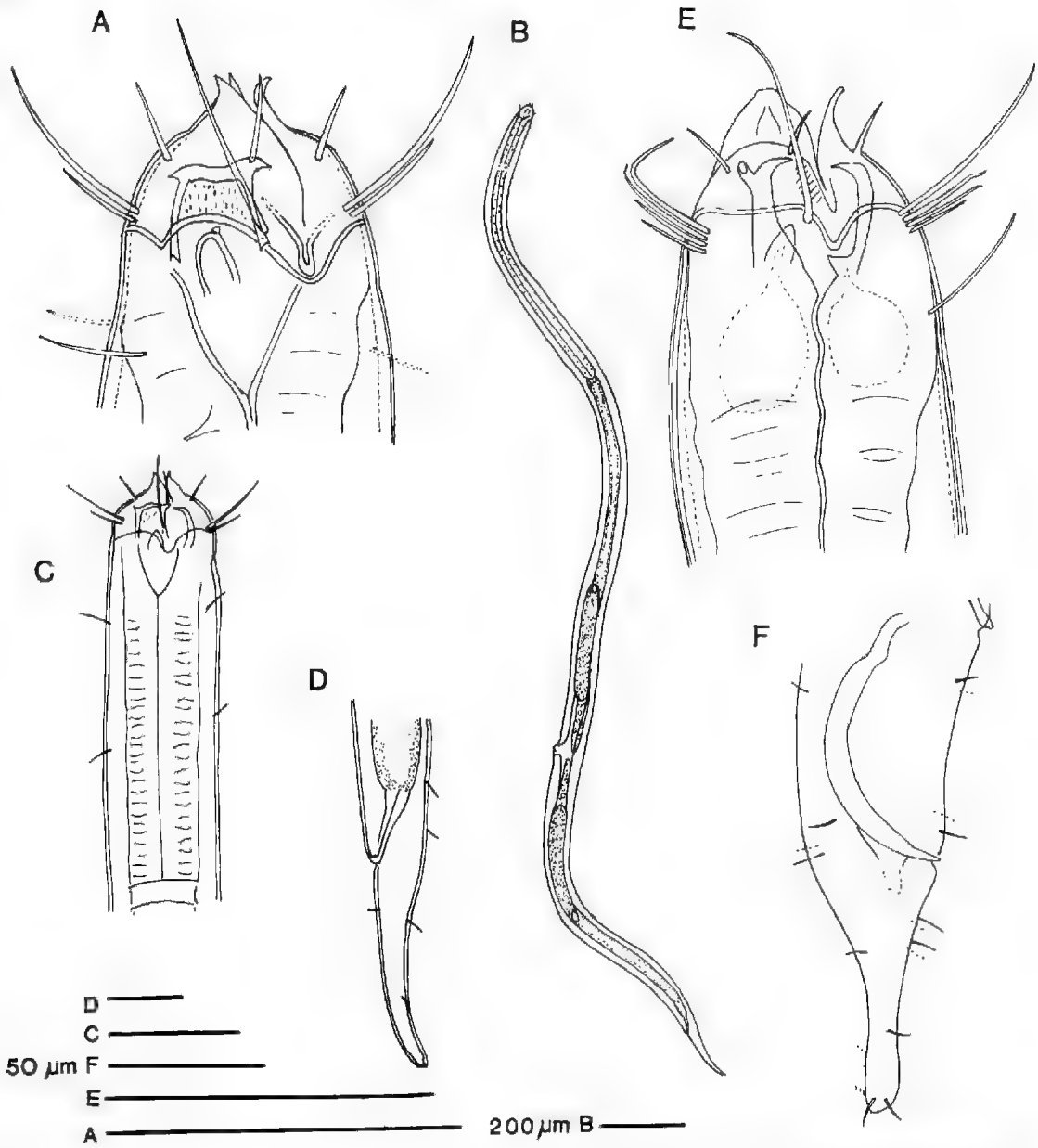

Fig. 2. *Mesacanthion alexandrinus* sp. nov. A, female head; B, entire female; C, head and cervical region; D, female tail. *Enoploides stewarti*. sp. nov. E, male head; F, tail and spicules.

Enoploides stewarti sp. nov.
FIGS 2, E, F, 3 A-E, Table 2

Types: Holotype: male, Lake Alexandrina, South Australia, 13.xii.1988, coll. W. L. Nicholas and A. F. Bird, in SAM 23880; paratypes: 2 males and 2 females, Lake Alexandrina, South Australia, 18.vii.1989, 5.x.1988, in SAM 23881-83; male and female, same location and collectors, 5.x.1988, W. L. Nicholas collection slide 1218.

Description of Holotype male. Body relatively plump, cuticle without annulation, scattered short setae along body. Cephalic capsule short, broad, height 0.38 times width at cephalic setae, three lips with deeply incised margins with striated borders, lips surmounted by thin flexible lip-flaps. Six labial setae (11 μm) at base of flaps, six long inner cephalic setae (31 μm) and four shorter outer cephalic setae (12 μm) inserted at base of cephalic capsule. Three mandibles characteristic of genus, lateral bars fused to form single rod, terminating in divergent hooks; three onchia at base of mandibles. Pharynx relatively long, muscular, cylindrical, terminating in conical cardia enclosed by anterior intestine. Two opposed testes, to right of intestine. Spicules uniformly curved, cyathiform, with proximal cylindrical knob. Supplementary organ inconspicuous, globular, 2.4 times body width at cloaca; gubernaculum a simple plate with very weak apophysis, caudal glands well developed, tail very short, conical, with swollen tip bearing three setae. Additional measurements in Table 2.

Paratypes: In males tail length is rather variable, as is distance of supplementary organ from cloaca. Females resemble males apart from sexual organs. Didelphic, ovaries opposed, antidromus, to right of intestine, each uterus with one large egg. See Table 2 for measurements.

Habitat: Freshwater, sand at waters edge of Lake Alexandrina, South Australia.

Comparison with other species: The genus *Enoploides* can be divided into two groups. One, comprising most of the 42 described species, possesses relatively long spicules, of the order of 300 μm, and a strong gubernaculum, the shape of which is of taxonomic value (Wieser & Hopper 1967). The other with relatively short spicules and a weak or rudimentary gubernaculum includes: *E. cirrhatus* Filipjev, 1918; *E. fluviatilis* Micoletzky, 1923; *E. caspersi* Riemann, 1966; *E. disparilis* Sergeeva, 1974; *E. alexandrae* Uzunov, 1974; *E. polysetosus* Jensen, 1986 and *E. stewarti* sp. nov.

E. caspersi can readily be distinguished from *E. stewarti* sp. nov. and others of this group by possessing a prominent post-anal organ. In *E. polysetosus* the spicules are longer (162-174 μm), thinner and almost straight, and the body carries many very fine somatic setae. Taxonomic differences between the other four species are given in Table 3.

The two freshwater species of *Enoploides*, *E. fluviatilis* and *E. stewarti* sp. nov. are very similar, though from widely separated localities, namely the

TABLE 2. *Measurements of* Enoploides stewarti *sp. nov.*

Type	holo	para	para	para	para	para
Slide	1160	1161	1218	1166	1165	1218
Sex	Male	Male	Male	Female	Female	Female
Length	3080	1930	2115	2750	2578	2510
Max. width	63	70	59	120	105	85
Labial setae	11	15	8	12	9	10
Inner cephalic	31	30	27	37	30	37
Outer cephalic	14	17	15	17	19	19
Mandible h×w	9×6	10×8	12×9	14×10	13×9	14×11
Head, h×w	11×35	10×35		14×49	11×44	16×42
Nerve ring	151	134	140	162	160	140
Pharynx	632	491	458	572	621	581
Vulva	-	-	-	1544	1458	1406
Tail	134	93	89	134	139	145
Width at anus	50	52	42	53	47	52
Spicules, arc	121	107	108	-	-	-
Supplement	118	78	100	-	-	-
Tail/anal breadth	2.68	1.79	2.12	2.53	2.96	2.79
Nerve ring/pharynx	0.24	0.27	0.31	0.28	0.25	0.24
L. ceph. setae/hw	1.07	0.86	0.79	0.75	0.61	0.88
Mandible h/w	0.67	0.75	0.79	0.75	0.69	0.79
Spicule/anal width	2.42	2.06	2.57			
De Man's ratio a	49	28	36	23	25	30
" b	4.9	3.9	4.6	4.8	4.2	4.3
" c	23	21	24	21	19	17
" c'	2.7	1.8	2.1	2.5	3.0	2.8
" V%				56	56	56

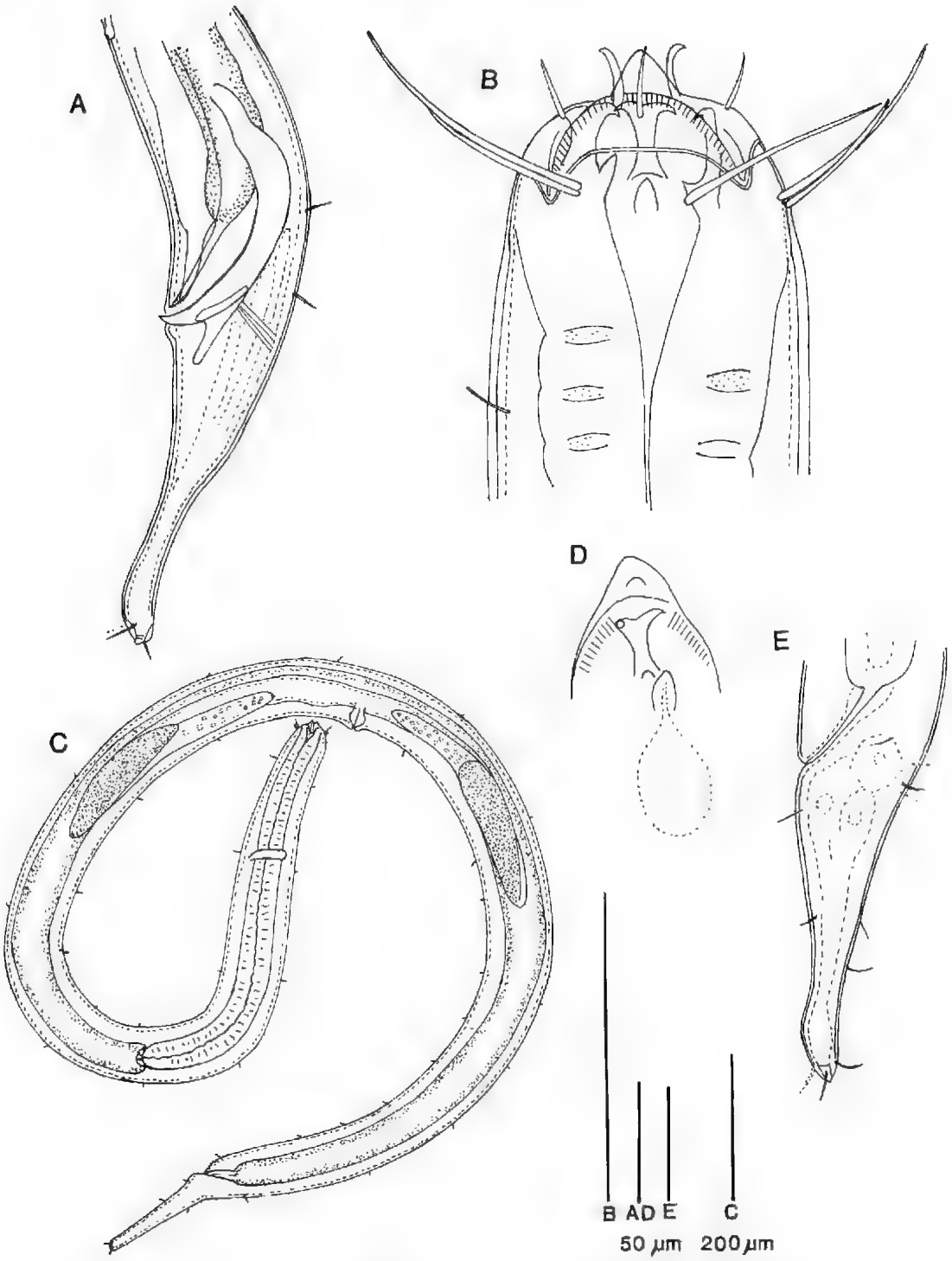

Fig. 3. *Enoploides stewarti* sp. nov. A, male tail; B, female head; C, entire female; D, mandible and onchium; E, female tail.

River Volga in Russia and the River Murray in Australia. In addition to Micoletzky's very full description, comparison between the two species has been facilitated by the loan of a male and female of *E. fluviatilis* from Russia by Dr Tsalolikhin. Both have shorter tails and longer spicules than others in this group, but because the males of *E. stewarti* show such significant differences in tail and spicule length, these characters cannot be used to separate the two species. The distance of the supplement from the cloaca also is too variable (118, 100 and 78 compared with 75 μm). However, the spicules of *E. fluviatilis* are transversely striated, terminal tail setae are lacking and there are two minute post-anal tail papillae, all differences from *E. stewarti* sp. nov.

Key to the males of *Enoploides* with short spicules, less than 300 μm

1. Spicules >150 μm, body hirsute, no post-anal organ ..... *E. polysetosus*
   Spicules <150 μm, not hirsute 2
2. Male with prominent post-anal organ ..... *E. caspersi*
   Male without such organ 3
3. Tail long (c<10, c' =7), no post anal setae ..... *E. disparilis*
   Tail long (c>10, c' =5) with pre- or post-anal setae or papillae 4
4. Tail medium c=10-16, c' <5 5
   Tail very short, c>16, c'<5 6
5. 7-8 pairs post-anal setae ..... *E. alexandrae*
   7 pairs pre-anal papillae ..... *E. cirrhatus*
6. Tail with two post-anal papillae, no terminal setae ..... *E. fluviatilis*
   Tail with 3 terminal setae, no post-anal papillae ..... *E. stewarti* sp. nov.

Discussion

Lake Alexandrina has been isolated from saline estuarine water for only 50 years, since the building of the barrages across the estuary of the River Murray. Possibly both species have become adapted to freshwater in the very short time since they were trapped above the barrages. However, no similar species were found below the barrages (Nicholas *et al.* 1992), nor have they been found in extensive collecting on nearby ocean beaches subsequently. Before the building of the barrages the outflow from the Murray was subject to great variations, and in droughts the flow of river water out of the estuary sometimes failed allowing sea water into the lake system. At times in the past when the climate was drier, these conditions may have persisted long enough for the adaptation of marine species to tolerate wide variations in salinity and eventually freshwater. It is not known whether any Thoracostomopsidae occur elsewhere in the Murray Darling system.

It is interesting that *E. stewarti* sp. nov. very closely resembles *E. fluviatilis*, from the River Volga in Russia, and is closer to *E. alexandrae* and *E. disparilis* from the Black Sea than congeners. Perhaps it was carried to South Australia on the bottom of ships, although the Murray mouth was not a useful port because of its treacherous and unreliable entrance. In this context it is interesting to note that specimens of *Oncholaimus dujardinii* described from Plymouth in the British Isles.

TABLE 3. *Features separating* Enoploides stewarti *sp. nov. and four similar species.*

	E. cirrhatus	*E. alexandrae*	*E. disparilis*	*E. fluviatilis*	*E. stewarti*
Cuticle	annulated	annulated	annulated	smooth	smooth
Spicule, arc	60	48/50	35	112	107-121
Spicule head	rounded	rounded	?	cylindrical	cylindrical
c	16	12	9.8	25	2.1-3.0/1.7-2.1
c'	?	5*	7.2*	3*	1.8-2.7/2.5-3.0

* Calculated from figures

TABLE 4. *Comparison between measurements of* Enoploides fluviatilis *and* E. stewarti *sp. nov.*

	Body	Tail	Spicules, arc	Supplement to cloaca
E. fluviatilis				
type	1610	60	112*	75*
range	1340-1900	54-61		
Male on loan	2219	67	91	60
E. stewarti sp. nov				
holotype	3080	134	121	118
2 paratype males	1930-2115	89-93	107-108	78-100
3 paratype females	2587-2749	134-145		

* Calculated from figures.

together with several other nematode genera, have been identified in scrapings from the bottom of sailing ships entering the port of Sydney from the British Isles (for Bicentenary celebrations) as part of an unpublished study by the Australian Museum. Studies of the as yet unexplored nematode fauna of Australian inland waters may throw fresh light on the natural history of the two new species.

Acknowledgments

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INTERSPECIFIC AND INTERGENERIC RELATIONS BETWEEN NEMATODES PARASITIC IN THE STOMACHS OF KANGAROOS AND WALLABIES

BY H. HOSTE & I. BEVERIDGE†*

Summary

Associations between conspecific and confamilial nematodes co-occurring at high prevalences in the stomachs of the eastern grey kangaroo, *Macropus giganteus,* from Victoria, the red kangaroo, *M. rufus* from New South Wales and rock wallabies of the *Petrogale assimilis* species complex *P. assimilis, P. sharmani* and *P. mareeba,* from Queensland, were investigated using principal components analysis. A similar pattern of associations was found in each host species, consisting mainly of positive associations between nematode species. Negative associations were found with *Rugopharynx australis* the numerically dominant nematode in *M. giganteus* and *M. rufus,* and to a lesser extent with *R. zeta* in *Petrogale* spp. The complex nematode communities present in each host were shown to be stable, with few negative associations between members.

KEY WORDS: *Macropus giganteus, Macropus rufus, Petrogale assimilis,* nematodes, communities, associations, multivariate analysis

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HOSTE, H. & BEVERIDGE, I. (1993) Interspecific and intergeneric relations between nematodes parasitic in the stomachs of kangaroos and wallabies. *Trans. R. Soc. S. Aust.* 117(4), 171-177, 30 November, 1993.

Associations between conspecific and confamilial nematodes co-occurring at high prevalences in the stomachs of the eastern grey kangaroo, *Macropus giganteus*, from Victoria, the red kangaroo, *M. rufus* from New South Wales and rock wallabies of the *Petrogale assimilis* species complex *P. assimilis*, *P. sharmani* and *P. mareeba*, from Queensland, were investigated using principal components analysis. A similar pattern of associations was found in each host species, consisting mainly of positive associations between nematode species. Negative associations were found with *Rugopharynx australis* the numerically dominant nematode in *M. giganteus* and *M. rufus*, and to a lesser extent with *R. zeta* in *Petrogale* spp. The complex nematode communities present in each host were shown to be stable, with few negative associations between members.

KEY WORDS. *Macropus giganteus*, *Macropus rufus*, *Petrogale assimilis*, nematodes, communities, associations, multivariate analysis

Introduction

Parasite communities in homeothermic animals are frequently complex in nature, with many species of parasites occurring in an individual host or host organ (Bush *et al.* 1990; Kennedy & Bush 1992). Because of the complexity of the community and, frequently, the large numbers of helminth species involved, the question as to whether community members interact or have interacted in the past to produce a stable, predictable structure or are non-interactive and result from a random collection of independent, individual species, has received considerable attention (see Holmes 1986; Price 1986). Evidence for the existence of interactive communities has been provided in the case of cestodes of ducks (Bush & Holmes 1986 a,b) and trichostrongyloid nematodes in sheep (Diez-Banos *et al.* 1992; Hoste & Cabaret 1992) while at the other extreme, the complex assemblages of monogenean parasites present as ectoparasites of fishes appear to exhibit few interactions (Rhode 1979; Koskivaara & Valtonen 1992; Koskivaara *et al.* 1992).

Amongst nematode parasites, the best known examples of complex parasitic communities existing within a single host organ are the oxyuroid nematodes of tortoises (Schad 1963; Petter 1966), and the strongyloid nematodes of elephants (Chabaud 1957), horses (Kennedy & Bush 1992) and kangaroos (Inglis 1971; Kennedy & Bush 1992). In the case of kangaroos, up to 40 species of nematodes, all belonging to a single order, the Strongylida, occur in the complex saccular fore-stomachs of individual host species (Spratt *et al.* 1990), with numbers of parasites reaching 300,000 or more (see Beveridge & Arundel 1979). Several studies (Mykytowycz 1964; Mykytowycz & Dudzinski 1965; Smales & Mawson 1978b; Arundel *et al.* 1979) have demonstrated that different species or genera of nematodes have different site preferences within the stomachs of kangaroos, as is the case with oxyuroid nematodes in tortoises (Schad 1963; Petter 1966), but there have been no studies undertaken to determine whether there is any evidence of interactions within these helminth communities.

Recently, Hoste & Cabaret (1992) have utilised a principal components analysis (PCA) and comparison with the model of Motomura (1947) in which the $\log_{10}$ abundance of a species is correlated with its rank in terms of abundance for examining the stability of nematode communities in sheep and the existence of interactions between the species or genera of parasites present with a host. In this paper, we apply their techniques to examine whether there is evidence of competitive interactions between the nematode parasites present in the stomachs of three taxa of macropodid marsupials.

Materials and Methods

Parasitological data

Data utilised in this study were obtained from earlier epidemiological studies on the parasites of macropodids.

The data for *Petrogale assimilis* included 35 specimens of *P. assimilis* as well as five specimens of what were formerly known as the Mt Claro and Mareeba chromosomal races of this species. They have recently been named *P. sharmani* and *P. mareeba* respectively (Eldridge & Close 1992). Rock wallabies were collected over an extensive area of northern and

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western Queensland (see Beveridge *et al.* 1989) during a study of the taxonomy of the hosts. Nematode taxa included in the study, their prevalence and mean intensity of infection are shown in Table 1. Any helminth species occurring outside the stomach, or at a prevalence of less than 10% e.g. *Cloacina similis, Coronostrongylus coronatus, Labiostrongylus bancrofti, Macropostrongylus petrogale* etc.) was not considered to be a core species (*sensu* Hanksi 1982) and was excluded from the statistical analyses. In addition, nematodes such as *Woodwardostrongylus oberndorfi* for which intensity data were not available, were also excluded. Since similarity coefficients for the helminth communities in *P. assimilis, P. sharmani* and *P. mareeba* are high (Beveridge *et al.* 1989), combination of their data was considered justifiable.

Data from *Macropus giganteus* were derived from an epidemiological study conducted at Yan Yean, Victoria, in which two adult and four juvenile kangaroos were collected at six-weekly intervals over a period of 10 months (Arundel *et al.* 1990). The prevalence and mean intensity of infection for the principal nematode species in the stomachs of these hosts are shown in Table 2. Any nematode species occurring in less than 10% of the host specimens (eg. *Alocoastoma clelandi*) was excluded from the analysis, as were the species of intestinal cestodes.

Data on the helminth parasites of *Macropus rufus* were collected at a single locality, Menindee, New South Wales (see Arundel *et al.* 1979), with 12 animals collected every two months, over a period of two years. Samples of kangaroos were collected within Kinchega National Park and on properties immediately adjacent to the Park. The only difference in prevalence detected was in the case of the bile duct inhabiting cestode *Progamotaenia festiva* (see Arundel *et al.* 1979). No differences were detected in the intensity of infection with any parasite. Hence it was considered valid to use combined data from the two adjacent collection localities (Table 3). Helminth parasites occurring at a low prevalence or intensity, such as the nematodes *Macropostrongyloides* spp., and *Hypodontus macropi* and the cestodes *Progamotaenia ruficola* and *Triplotaenia undosa* were excluded from the analysis.

Changes in the nomenclature of parasites since the publication of the original epidemiological papers have been indicated in Tables 1-3, together with appropriate references. In *M. giganteus*, individuals of the genus *Labiostrongylus* and in *M. rufus* and *M. giganteus* members of the genus *Cloacina* were not identified in a quantitative fashion to species level, because of inadequate information on the taxonomy of these genera, though the species present at each locality were recorded. In *M. giganteus*, most of the species of *Cloacina* present are undescribed.

TABLE 1. *Prevalence and intensity of infection of the principal nematode parasites present in the stomach of 39* Petrogale assimilis, P. sharmani *and* P. mareeba *from Queensland.*

Parasite species	Prevalence (%)	Mean Intensity
Rugopharynx zeta (Johnston & Mawson, 1939)	53	2,190
Cloacina petrogale Johnston & Mawson, 1938	72	390
C. pearsoni Mawson, 1971	98	980
C. parva Johnston & Mawson, 1938	100	780
C. hydriformis Johnston & Mawson, 1938	46	200
Cl. sp. (undescribed) (*C. sp. 1* of Beveridge *et al.* 1989)	54	420
Filarinema spp. (*F. dissimile* (Wood, 1931), *F. austrole* (Wood, 1931), *F. nunwonae* Cassone & Baccam, 1985)	33	13

TABLE 2. *Prevalence and intensity of infection of the principal nematode parasites present in the stomach of 45* Macropus giganteus *from Yan Yean, Victoria.*

Parasite species	Prevalence (%)	Mean Intensity
Rugopharynx australis (Mönning, 1926)	100	46,290
R. rosemariae Beveridge & Presidente, 1978	27	2,210
Cloacina spp. (*C. obtusa* Johnston & Mawson, 1939, *C.* cf. *hydriformis* Johnston & Mawson, 1938, *C.* cf. *elegans* Johnston & Mawson, 1938)	98	7,630
Labiostrongylus spp. (*L. bipapillosus* (Johnston & Mawson, 1938), *L. kangi* Mawson, 1955)	73	260
Pharyngostrongylus kappa Mawson, 1965	85	9,350
Strongyloides sp. (undescribed)	59	835

TABLE 3. *Prevalence and intensity of infection of the principal nematode parasites present in the stomach of 100* Macropus rufus *from Menindee, New South Wales*

Parasite species	Prevalence (%)	Mean Intensity
Rugopharynx australis (Mönning, 1926)	99	51,850
Willabinema cobbi (Kung, 1948) (syn. *Zoniolaimus cobbi*)	84	9,655
Cloacina spp. (*C.* cf. *hydriformis* Johnston & Mawson, 1938, *C. expansa* Johnston & Mawson, 1939, *C. macropodis* Johnston & Mawson, 1938)	71	3,090
Labiostrongylus longispicularis Wood, 1931	88	332
Filarinema spp. (*F. flagrifer* Mönning, 1929, *F. austrole* (Wood, 1931))	92	79
Papillostrongylus sp. (undescribed) (= *P. labiatus* Johnston & Mawson, 1939 *sensu* Arundel *et al.* 1979)	41	1,680

Statistical methods

For each host species, a separate principal component analysis (PCA) was performed, using the STATITCF computer program (1988), on both the intensity data (*sensu* Margolis *et al.*, 1982) and the frequency data defined as the number of nematodes of a particular species expressed as a percentage of the total number of worms within that host. The data were standardised prior to analysis as (actual value − mean value for the variable) ÷ standard error for the variable.

The data were arranged in a correlation matrix whose columns (variables) were the parasite species and rows were the individual animals. Component axes were defined from correlations between the variables (parasite species numbers). The coordinates of each variable were then expressed in relationship to the new axes. Axes 1 to 3 were studied, the percentage of variability accounted for by each axis being indicated for each PCA in Table 4.

TABLE 4. *Percentage of total variability expressed by component axes 1, 2 and 3 following Principal Component Analysis (PCA) of the intensity and frequency of infection of* Petrogale spp., Macropus giganteus *and* M. rufus *with nematode parasites.*

Host species	Axis 1	Axis 2	Axis 3	Total (1 + 2 + 3)
Petrogale spp.				
Intensity	34.4	22.0	18.7	75.1
Frequency	31.6	23.8	19.2	74.6
Macropus giganteus				
Intensity	28.0	24.5	18.4	70.9
Frequency	33.6	21.3	18.3	73.2
Macropus rufus				
Intensity	37.0	19.7	16.8	73.5
Frequency	31.2	18.6	18.0	67.8

For each host species and each set of data, i.e. intensity and frequency, Euclidean distances between parasite species were calculated by applying Pythagoras' theorem to the coordinates of each variable, i.e. parasite species, was located within the three dimensional space constructed by axes 1 to 3 (Table 5). These distances characterised quantitatively the relation between nematode species. The minimum value for these distances was 0, the maximum 2. Distance values > 1.2 and < 0.8 are considered indicative of negative and positive interactions between species respectively (Hoste & Cabaret 1992).

In each host species, the distances between each pair of nematode species were calculated in the three planes and the result was called D_2. These D_2 distances were fitted to the logarithmic model of Motomura (1947) i.e. the decimal logarithms of distances were regressed on the rank of each species pair. According to Motomura's (1947) model, the $\log_{10}$ of the abundance of a species is correlated with its rank in the order of most abundant to least abundant species.

In addition, in order to represent the relation of one particular species to others present in the stomach, mean distances were calculated as the averages of the D_2 distances for each pair of worm species including the particular species of interest. These mean distances were called D_5 in both species of kangaroos as they were distances between a given parasite taxon and five others, and called D_6 in the case of the rock wallabies since the distance was from six other taxa.

TABLE 5. *Coordinates of nematode species on component axes 1, 2 and 3 following a Principal Components Analysis (PCA) performed on the intensity and frequency of infection of* Petrogale spp., Macropus giganteus *and* M. rufus, *with nematode parasites.*

Host	Parasite	Intensity Data			Frequency Data		
		Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Petrogale spp.	*Cloacina sp.* 1	-0.625	0.311	0.497	0.382	0.070	0.772
	C. hydriformis	-0.218	-0.813	-0.084	-0.338	-0.768	0.124
	C. parva	-0.783	0.298	-0.448	-0.629	0.501	-0.453
	C. pearsoni	0.863	0.179	-0.394	-0.743	0.319	0.409
	C. petrogale	-0.456	-0.785	0.137	-0.224	-0.838	-0.248
	Rugopharynx zeta	-0.636	-0.081	0.505	0.912	0.039	-0.112
	Filarinema spp.	-0.024	0.198	0.653	0.349	0.120	-0.538
Macropus giganteus	*Rugopharynx australis*	0.653	0.594	0.169	0.954	-0.244	0.051
	P. kappa	-0.305	0.262	0.673	-0.109	0.876	-0.220
	Cloacina spp.	-0.374	0.714	-0.294	-0.906	-0.248	0.039
	Labiostrongylus spp.	-0.370	-0.077	0.688	0.076	0.614	0.450
	R. rosemariae	-0.517	0.647	-0.135	-0.444	-0.120	0.582
	Strongyloides sp.	0.785	0.337	0.216	-0.264	-0.010	-0.710
Macropus rufus	*Labiostrongylus longispiculatus*	0.004	0.391	0.878	0.162	-0.088	0.622
	Filarinema spp.	-0.686	0.060	0.014	-0.487	-0.844	0.141
	Rugopharynx australis	-0.900	-0.133	0.087	0.988	0.037	-0.132
	Cloacina spp.	-0.503	0.627	-0.019	-0.318	0.419	0.578
	Wallabinema cobbi	-0.819	-0.159	-0.167	-0.050	0.259	0.386
	Papillostrongylus sp.	-0.138	-0.769	0.452	-0.728	0.393	-0.417

Results

Average distances of individual species from remaining species (D_5 and D_6)

Comparison of the mean euclidean distances for each worm species with related species in the three different hosts showed several similarities (Fig. 1). Firstly, in the three host species, the mean distances calculated from the frequency data were generally higher than those calculated from the intensity data. Secondly, no mean distances calculated from intensity or frequency data exceeded 1.2 which is suggestive of no negative association between species. Thirdly, based on the frequency data, the highest values of D_5 were associated with the species *Rugopharynx australis* in both of the kangaroo species. Though not so marked, a similar situation prevailed with *R. zeta* in rock wallabies having a D_6 value as high as any other of the other associations.

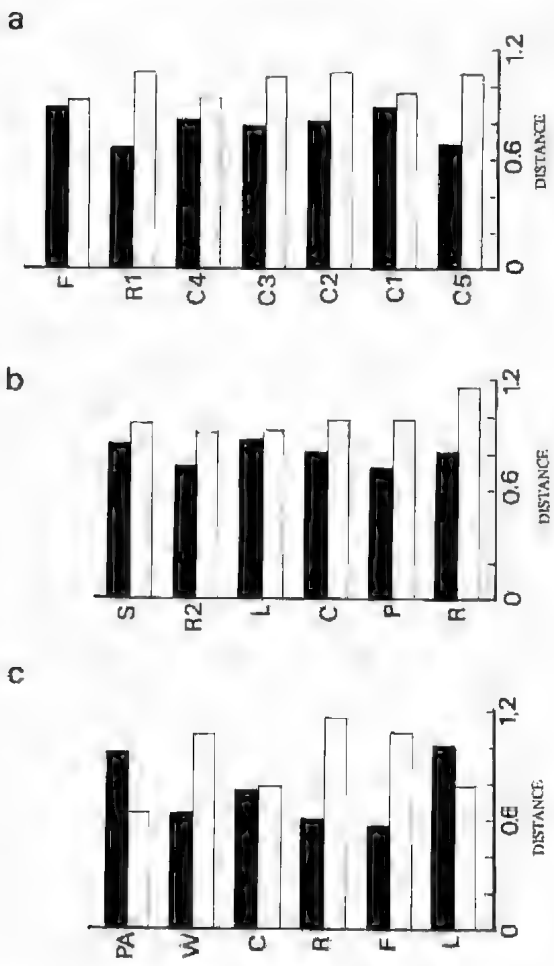

Fig. 1. Mean distances (D_5 & D_6) between individual parasite taxa, based on both intensity (closed histograms) and comparative frequency of occurrence (open histograms) in (a) *Petrogale* spp., (b) *Macropus giganteus* and (c) *M. rufus* calculated from principal components analysis (PCA).
Legend: C, *Cloacina* spp.; C1, *Cloacina hydriformis*; C2, *C. parva*; C3, *C. pearsoni*; C4, *C. petrogale*; C5, *C.* sp.; F, *Filarinema* spp.; L, *Labiostrongylus* spp.; PA, *Papillostrongylus* sp.; P, *Pharyngostrongylus kappa*; R, *Rugopharynx australis*; R1, *R. zeta*; R2, *R. rosemariae*; S, *Strongyloides* sp.; W, *Wallabinema cobbi*.

Average distances between species pairs (D_2 distances)

Comparison of the ranked D_2 distance distributions in the three host species added to the results obtained by analysis of the D_5 and D_6 distances. In the PCA performed on the frequency data (Fig. 2), the rank distribution of the D_2 distances for the 15 pairs of worm species in the red and grey kangaroos, and for

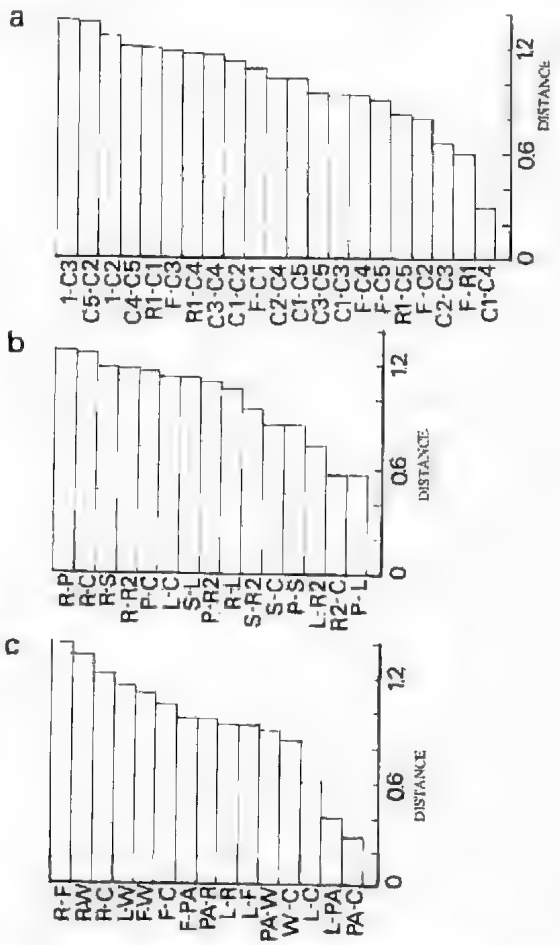

Fig. 2. Ranked distances (D_2) between parasite species pairs based on comparative frequency of occurrence in (a) *Petrogale* spp., (b) *Macropus giganteus* and (c) *M. rufus* calculated from principal components analysis.
Legend: as for Fig. 1.

the 21 pairs in the rock wallabies fitted Motomura's model. Additionally, some of the distances between nematode species were high (> 1.2) which suggests negative interactions. This observation was made in the three different host species, and among those pairs exhibiting the highest distance values, *Rugopharynx* spp. were usually present. These results suggest that *Rugopharynx* was negatively associated with the other worm species based on the frequency analysis.

The D_2 distances calculated from the intensity data (Fig. 3) were lower than those obtained from PCA performed on the frequency data. In the three different host species, the D_2 distances were less than 1.2, and usually less than 1.0, which tends to indicate the lack of any significant negative association between nematode species. The rank distribution of patterns of these D_2 distances also fitted Motomura's model. When compared to the distribution of the D_2 distances obtained from the frequency analysis, the order of the different pairs in the intensity data was distinct, with a less well defined ranking of *Rugopharynx australis*.

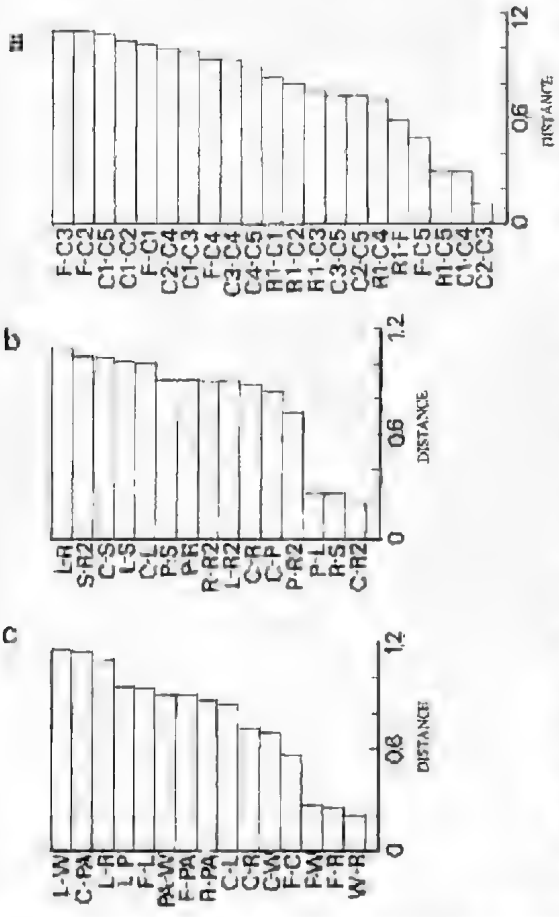

Fig. 3. Ranked distances (D_2) between parasite species pairs based on intensities of infection in (a) *Petrogale* spp., (b) *Macropus giganteus* and (c) *M. rufus* calculated from principal components analysis.
Legend: as for Fig. 1.

Discussion

The results of analysis both of frequency and intensity of infection data for all three species of macropodid hosts can be fitted to Motomura's model (1947) for density associations between populations of similar species within the same biotope and suggest the existence of stable nematode communities in the stomachs of the macropodid species examined. Furthermore, most of the D_2 distances calculated on the intensity data were less than 1.0 and even less than 0.8. As these distances are thought to reflect the intensity of parasitism at the suprapopulation level or host population level, this fact provides additional evidence of the preponderance of positive associations between component species and hence infers the existence of stable communities. Positive associations are known to occur in the case of other host groups acquiring their parasite infections from grazing pastures contaminated with various species of infective third stage larvae of nematodes such as ruminants (Diez-Banos *et al.* 1992; Hoste & Cabaret 1992). On the other hand, the frequency-based distances mainly reflect the infracommunity present in the individual host, and the fact that the frequency-based distances were generally greater than those derived from intensity data suggests that additional regulatory factors are involved at the suprapopulation level, as occurs also in the case of ruminants (Hoste & Cabaret 1992). The regulation of nematode populations in kangaroos is not well understood. Smales & Mawson (1978) and Arundel *et al.* (1990) demonstrated that in the case of the Tammar wallaby, *M. eugenii* and eastern grey kangaroo *M. giganteus*, in winter rainfall areas of South Australia and Victoria, there was an increase in the number of nematodes present in the stomach during the moist winter months which is the most favourable period of the year for larval development in the external environment. Arundel *et al.* (1990) also demonstrated an effect of host age on certain species of nematodes (e.g. *Rugopharynx rosemariae*), with juvenile animals exhibiting a higher prevalence and intensity of infection, while in other nematode genera (*Cloacina*, spp., *R. australis*) intensity was higher in adult hosts. By contrast, the study by Arundel *et al.* (1979) on the red kangaroo, *M. rufus*, in the arid, non-seasonal rainfall region of western New South Wales indicated in the case of several of the dominant nematode species (*R. australis*, *Wallabinema cobbi*) that there was no seasonal effect on intensity of infection and that intensity of infection increased linearly with host age. In all of these three *Macropus* species, *Labiostrongylus*

spp. exhibited an unique pattern of development, with larval stages maturing over a period of several months during the summer (Mykytowycz & Dudzinski 1965; Smales & Mawson 1978a; Arundel *et al.* 1979). Because of the lack of detailed knowledge of the way in which nematode populations in kangaroos are regulated, it is difficult to explain what the additional regulatory factors at the suprapopulation inferred by the present analysis might be. However, Petter (1966) also found an effect of host age and season on interactions between the oxyuroid nematodes of tortoises, suggesting that these might be general phenomena.

In contrast to other studies on gastro-intestinal strongylid nematodes (Hoste & Cabaret 1992; Diez-Banos *et al.* 1992), analysis of populations of the stomach-inhabiting nematodes parasitic in three species of macropodid hosts failed to reveal evidence of extensive negative interactions between nematode species. The only suggestion of negative associations involved *Rugopharynx australis* in red and grey kangaroos, and in both of these kangaroos, *R. australis* is numerically the dominant stomach nematode (Arundel *et al.* 1979, 1990; Beveridge & Arundel 1979). In the case of the rock wallabies no particular dominant species emerged. *Rugopharynx zeta* occurred at a higher intensity in rock wallabies than other gastric nematodes, but occurred at a prevalence of only 50%. *Cloacina pearsoni* and *C. parva* by contrast occurred in 100% of the hosts examined but at a lower intensity. The differences in intensity and prevalence may counteract one another to present a community in which there are few negative interactions. An additional consideration when comparing data from rock wallabies with that from the kangaroos is that in the former case, hosts were collected over a wide area of northern Queensland, compared with single localities for each of the kangaroo species.

Negative associations are evident in the frequency data only, which refers essentially to the infrapopulation at the individual host level: there is no such evidence from analysis of the raw intensity data, which relates to the parasite suprapopulation or the host population level. However, Holmes (1986) has cautioned that interactions are frequently obscured when suprapopulations are considered and that the optimum method for detection of interaction is at the infrapopulation level, a conclusion which is clearly supported by the current results.

Thus, the nematode communities present in the three species of macropodids examined here demonstrate similar features in being stable, and probably mainly non-competitive communities, with the exception of *Rugopharynx australis*. This lack of negative associations contrasts sharply with the results of Bush & Holmes (1986a) from studies on the cestodes of ducks and those of Hoste & Cabaret (1992) and Diez-Banos *et al.* (1992) for ruminants. Rohde (1979) suggested that in non-interactive communities not all niches are filled, there is no basis for competition and differential localisation of parasites occurs because it facilitates reproduction rather than minimises competition. Rohde's hypothesis (1979) is therefore consistent with the data currently available for nematode communities parasitic in the stomachs of macropodids. The kangaroo stomach is a relatively enormous organ in comparison with the size of parasites, and data from various sources (e.g. Beveridge & Arundel 1979) suggests that healthy macropodids are capable of harbouring numbers of nematodes far in excess of those encountered in this study. Hence it is not unreasonable to assume that vacant niches are abundant within kangaroo stomachs, given the proviso that nematode numbers only have been examined, without any consideration of their relative biomass. Whether the differential localisations of nematodes observed are due to reproductive strategies or due to the presence of competition in the past, during the evolution of the parasite community structure, is not clear.

Price (1986) predicted that considerable variation in community characteristics might be expected when a sufficiently wide range of communities was examined. The present results indicate that speciose nematode communities of homoeothermic vertebrates, while stable in their structure, may not necessarily display significant negative associations between their component members.

Acknowledgments

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EFFECT OF *ACROBELOIDES NANUS* (NEMATODA: CEPHALOBIDAE) UPON THE OF *PSEUDOMONAS CORRUGATA* (EUBACTERIA) IN PASTEURIZED SOIL FROM KAPUNDA, SOUTH AUSTRALIA

BY MAARTEN H. RYDER† & ALAN F. BIRD**

Summary

Acrobeloides nanus and *Pseudomonas corrugata* were co-inoculated into the same pasteurized field soil. The population of the nematode increased ten-fold in eight weeks, whereas the population of the bacteria decreased with time, in all cases. After eight weeks at 15°C, the population of the introduced bacteria was significantly lower where *A. nanus* had been added to the soil. At 22°C the population of *P. corrugata* was much lower irrespective of the presence or absence of *A. nanus.* The feeding of nematodes on bacteria in soil helps to explain the observed decrease in the population of microbial control agents introduced into the soil in field experiments.

KEY WORDS: *Acrobeloides nanus,* bacteria, biological control, Cephalobidae, nematodes, *Pseudomonas corrugata,* soil, take-all.

Transactions of the Royal Society of S. Aust. (1993), 117(4), 179–182.

EFFECT OF *ACROBELOIDES NANUS* (NEMATODA: CEPHALOBIDAE) UPON THE SURVIVAL OF *PSEUDOMONAS CORRUGATA* (EUBACTERIA) IN PASTEURIZED SOIL FROM KAPUNDA, SOUTH AUSTRALIA

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Summary

RYDER, M. H. & BIRD, A. F. (1993) Effect of *Acrobeloides nanus* (Nematoda: Cephalobidae) upon the survival of *Pseudomonas corrugata* (Eubacteria) in pasteurized soil from Kapunda, South Australia. *Trans. R. Soc. S. Aust.* 117(4), 179–182, 30 November, 1993.

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KEY WORDS: *Acrobeloides nanus*, bacteria, biological control, Cephalobidae, nematodes, *Pseudomonas corrugata*, soil, take-all.

Introduction

With increased interest in the use of biological control agents as alternatives to chemical control measures has come an interest in the fate of these biocontrol agents in the soil. In particular, information on the effect that bacterial-feeding nematodes may have on bacterial biocontrol organisms is sparse. Accordingly, we have isolated, cultured and microscopically examined a biocontrol bacterium and a nematode from the same agricultural soil and have studied their relationship both on agar plates and in the soil.

The bacterium *Pseudomonas corrugata* isolate 2140R is a biocontrol agent against the root-pathogenic fungus *Gaeumannomyces graminis* var. *tritici* (Ryder & Rovira 1993). This fungus causes the root disease take-all which is responsible for serious yield losses in cereal crops in southern Australia and elsewhere in the world. *P. corrugata* 2140R is a rifampicin-resistant derivative of the parent strain and is, therefore, easily identified. The nematode which we used was *Acrobeloides nanus* (Anderson 1968; Boström & Gydemo 1983; Nicholas & Stewart 1989; Bird *et al.* 1993), a cosmopolitan, bacterial-feeding, free-living organism that is widespread in agricultural and arid soils throughout Australia. The nematode *A. nanus* can use the bacterium *in vitro* as a nutrient source and is able to complete its life cycle and reproduce while feeding only upon *P. corrugata* (Bird & Ryder 1993). We show that the presence of *A. nanus* can lead to a reduction of bacterial numbers when both organisms are inoculated into pasteurized soil.

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Materials and Methods

Nematode

Acrobeloides nanus was isolated, by means of a misting apparatus, from the dry soil, collected six years previously (in 1986), from which *P. corrugata* had originally been isolated (Bird & Ryder 1993).

Bacteria

Pseudomonas corrugata 2140 was isolated originally from the rhizosphere of wheat seedlings that had been grown in a field soil, a red-brown earth pH 6, collected from Wagga Wagga, New South Wales (Ryder & Rovira 1993). The rifampicin-resistant derivative *P. corrugata* 2140R was isolated as a spontaneous mutant growing on Nutrient Agar, by J. Brackin, Monsanto Co., St Louis, USA.

Soil and pasteurization conditions

Field soil, a sodic red-brown earth (Stace *et al.* 1968), more recently defined as a fine mixed thermic calcic natrixeralf (Soil Survey Staff 1990), from Kapunda, South Australia, that had been air-dried and sieved (<3 mm) was used in our experiments. Immediately prior to use, it was steam sterilized at 75°C for 15 min in order to kill all nematodes but not all bacteria.

Inoculation of soil with bacteria and nematodes

Treatments consisted of nematodes + bacteria (+N+B), nematodes alone (N), bacteria alone (B) and controls without either. Each treatment was replicated five times. The experiments were run at 15°C and 22°C and were harvested at eight weeks from commencement.

The nematodes, grown on *P. corrugata* 2140, the parent bacterial strain which is sensitive to

rifampicin, on malt extract agar (Oxoid) were washed from the Petri dishes with sterile distilled water, centrifuged three times in sterile distilled water (200 × *g* for 10 min) and added as aliquots to the soil samples. In the +N+B treatment, bacteria were added to the suspension of nematodes immediately prior to inoculation of the soil. At the commencement of the experiment, samples (20 g) from all four treatments were placed on a misting nematode-extraction apparatus and the nematodes in the eluate were counted. The +N+B treatment yielded four nematodes per g of dry soil, and +N alone five. No nematodes were found in the soils with added bacteria (+B) or in the controls (C).

Bacteria (*P. corrugata* strain 2140R) were grown on Nutrient Agar (Difco), containing rifampicin (Boehringer) at 100 mg per litre, for two days at 25 °C. The cells were harvested by washing the plate with 4 ml sterile distilled water. The cell density was adjusted to ca. 2×10^7 colony-forming units (cfu) per ml before inoculation of soil. The starting population of *P. corrugata* was taken as the number of rifampicin-resistant bacteria recoverable from the soil 30 min after inoculation. Five replicate samples were processed for dilution plating. The initial bacterial populations were 1.5×10^6 cfu/g dry soil (+B) and 1.17×10^6 cfu/g dry soil (+N+B).

The air-dried soil was wet initially to 12% (w/v) with distilled water. 20 g portions of moist soil were dispensed into sterile containers (plastic-capped, 120 ml capacity). Either nematodes (+N) or bacteria (+B) alone were added to the soil in 1 ml. For addition of both organisms together (+N+B), the suspensions of nematodes and bacteria were mixed and then added to the soil in 1 ml. Sterile distilled water (1 ml) was added to the control treatment. The organisms were mixed into the soil thoroughly using a glass rod that had been wiped with ethanol, but the mixing was done gently to preserve the nematodes. The final water content of the soil was 19.4% (w/w dry soil).

Incubation conditions

The containers with treated soil were incubated in darkness at either 15 °C or 22 °C. They were capped tightly, but once each week the lids were removed for several seconds in a laminar flow cabinet, to allow gas exchange to occur. The incubation period was eight weeks.

Isolation and enumeration of bacteria

Sterile distilled water was added to each container so that the total volume of soil and liquid was 70 ml. The container was shaken gently for 30 sec to allow the soil aggregates to disperse. One ml was taken for analysis of bacterial populations by dilution plating. The selective medium used was Nutrient Agar containing cycloheximide (75 mg/l) and rifampicin (100 mg/l). The droplet plating method (three replicate 10 µl droplets) was used except for the controls (C) where 0.1 ml of the undiluted suspension was spread on the plate. Bacterial colonies were counted after two days at 25 °C.

Isolation and counting of nematodes

The nematodes in the remaining 69 ml of soil suspension were isolated by means of Seinhorst's two flask technique followed by sieving and counting (Hooper 1986).

Statistics

Populations of nematodes and bacteria were analysed by an analysis of variance of log-transformed data (Genstat Version 5).

Results

The populations of both *A. nanus* and *P. corrugata* after eight weeks in pasteurized Kapunda soil at 15 °C or 22 °C are shown in Figs 1 & 2. There were no significant differences in populations of *A. nanus* at either temperature after eight weeks (bacterial treatment: $F=0.18$, $p=0.68$; temperature: $F=1.29$, $p=0.27$). Where nematodes were added their numbers had increased at least ten-fold since the commencement of the experiment. Addition of *A. nanus* significantly

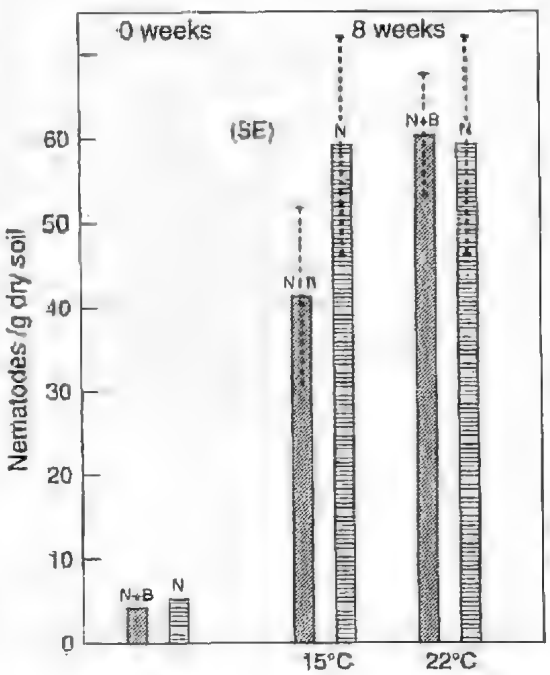

Fig. 1. Histogram showing no significant difference in numbers of nematodes at either temperature after eight weeks irrespective of whether bacteria were added or not. Error bars represent standard error (SE) of the mean.

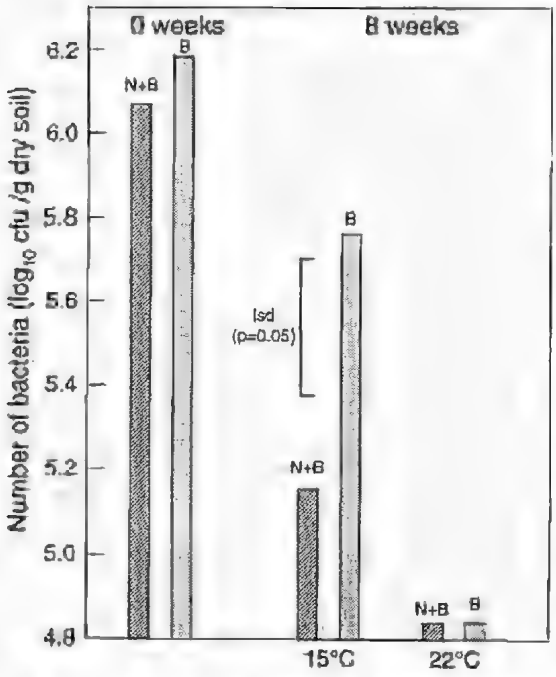

Fig. 2. Histogram showing a significant decrease in bacterial numbers after eight weeks at 15°C when nematodes were present.

reduced the population of *P. corrugata* over eight weeks at 15°C (nematode treatment: $F=13.49$, $p<0.001$; temperature: $F=18.53$, $p<0.001$; interaction between nematode treatment and temperature: $F=3.76$, $p=0.038$). Numbers of *P. corrugata* decreased eight-fold in the presence of *A. nanus* compared to two and three quarter-fold in the absence of the nematode. At 22°C over this period of time, bacterial numbers were reduced, to approximately one twentieth of the population at the start of the experiment, irrespective of whether or not nematodes were present.

Discussion

The presence of *A. nanus* in the soil significantly reduced the population of *P. corrugata* after eight weeks at 15°C. This temperature closely resembles winter soil temperatures in the field in South Australia, when biological control of *G. graminis* var. *tritici* by *P. corrugata* has been tested. Our results provide a possible explanation for the observed decrease in numbers of pseudomonads in biocontrol experiments conducted in the field (Weller 1983; Ryder *et al.* 1990).

After eight weeks at 22°C, the numbers of *P. corrugata* were much reduced. This occurred irrespective of whether *A. nanus* was present or not. This suggests that competition with other bacteria, with growth optima close to 22°C, may be responsible for the decline in numbers of *P. corrugata* in the soil. This decrease in numbers of *P. corrugata* is probably not due to increased temperature because its growth rate *in vitro* is higher at 20-30°C than at 15°C (Ross & Ryder, unpubl.).

Pasteurization of the soil resulted in the death of all soil nematodes and many, but not all, of the bacteria. This meant that the *P. corrugata* were introduced into a bacteriologically competitive soil environment. One such competitor, yet to be identified, proved to be a bacterium that formed visible white patches on the surface of the soil. These patches were considerably reduced in the presence of the nematodes and were presumably fed upon by *A. nanus*.

The bacterial-feeding nematode *A. nanus* is both widespread in South Australian agricultural soils and is relatively abundant, forming 12-28% of the total nematode fauna in soil from field plots at Kapunda, SA, sampled in the spring of 1992 (Yeates & Bird in press). This is equivalent to 1-17 nematodes per gram of dry bulk soil. Thus the levels of added *A. nanus* in the experiment reported here, were representative of numbers found naturally in the field.

The ability of *A. nanus*, and other species of bacteria-feeding nematodes, to graze on bacteria may affect the biocontrol performance of introduced bacteria. This may be particularly important for introduced bacteria in the rhizosphere, as there is evidence that bacteria-feeding nematodes can inhabit the rhizosphere in large numbers (Griffiths 1990). The relative populations of bacterivorous nematodes in the rhizosphere and bulk soil should also be of great interest to those who wish to introduce specific bacterial strains into the rhizosphere. Whether the effect of *A. nanus* in decreasing populations of *P. corrugata* can be large enough to decrease biocontrol performance in a natural soil is not yet known.

Interactions between rhizosphere or soil bacteria and plant pathogenic nematodes have been studied by Bookbinder *et al.* (1982). In their study, there were synergistic negative effects when the bacterial strains, including *P. corrugata* isolated from symptomless alfalfa roots, were inoculated together with a range of plant pathogenic nematodes. However, as far as we are aware, ours is the first report of the relationship between a specific soil bacterium and a bacteria-feeding nematode isolated from the same soil. Further studies along these lines with microbivorous nematodes and the bacteria upon which they feed are necessary steps in understanding both the complexity of the interactions between these organisms in the soil environment and the limitations on the success of biocontrol agents in controlling disease. Further research on these lines is also warranted because these nematodes are readily cultured, natural inhabitants of the soil whose inundative release in other situations may prove to be of immense benefit in maintaining soil fertility while reducing the numbers of undesirable microorganisms.

Acknowledgments

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THE BIG ROCK DONGA METEORITE: A NEW H5 CHONDRITE FROM SOUTH AUSTRALIA

*BY M. ZBIK**

Summary

The Big Rock Donga meteorite is a stone with a total weight of 11 kg found north of Fisher, South Australia, in 1989. It has been classified as a H5 chondrite and contains olivine ($FA_{18.8}$), orthopyroxene ($FS_{16.9}$), plagioclase ($An_{14}Or_{6.1}Ab_{79.9}$), clinopyroxene, nickel-iron, troilite, and chromite. Mineral compositions and textures indicate that the Big Rock Donga meteorite was a metamorphosed part of the H-planetoid and was very weakly shocked before reaching Earth.
KEY WORDS Big Rock Donga, meteorite, chondrite.

Transactions of the Royal Society of S. Aust. (1993), 117(4), 183–185.

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KEY WORDS: Big Rock Donga, meteorite, chondrite.

Introduction

The Big Rock Donga meteorite was found in 1989 by an unknown collector, north of Fisher on the South Australian part of the Nullarbor Plain. It has a total weight of 11 kg (South Australian Museum records) but is now in several pieces. The approximate co-ordinates for the site are 30°33′S, 130°58′E. The meteorite was collected illegally and exported to the United States of America, but we have obtained a 37 gram slice from an American mineral dealer, Mr David New. According to McCoy (1991, & pers. comm. 1993) the meteorite weighed 19 kg initially and was recovered as a single stone 16 km north of Fisher by a rabbit trapper (who wanted to remain nameless).

In recent years the Nullarbor Region has proved to be a productive area for the recovery of meteorites (Bevan 1992; Bevan & Binns 1989a, b) and in the last few years has attracted the attention of illegal meteorite collectors. Under legislation enacted by the Governments of Western Australia and South Australia all meteorites found in these states are the property of the Crown. An unfortunate consequence of the illegal trade in meteorites is the loss of important information on the exact date and location of the find.

Physical description

The stone is not heavily weathered but displays iron staining of the silicate minerals and fractures filled with iron oxides especially near the fusion crust. The interior of the meteorite is dark grey to black in colour and medium to fine grained with heavy fine grained nickel-iron metallic inclusions. In thin section the meteorite is generally light coloured (Fig. 1). The chondrules are recrystallised and have poorly defined boundaries but are recognisable under crossed polars. They are typically 0.5 mm in diameter. Metal and troilite occur as finely disseminated grains throughout the matrix. One piece of the slice was cut and a polished thin section was prepared and used for petrographic examination and in electron microprobe analyses.

Mineralogy

Compositions of the silicate minerals were determined with a JEOL electron microprobe at the University of Adelaide Centre for Electron Microscopy and Microbeam Analysis. Analyses were made using an accelerating voltage of 15 kV, a sample current of 3 nA, and a beam width of 5 μm. Representative mineral analyses are presented in Table 1.

Relic chondrules and chondrule fragments are composed predominantly of olivine with lesser amounts of orthopyroxene. The majority of chondrules are porphyritic in texture containing euhedral olivine crystals up to 0.2 mm in length set in a matrix of

TABLE 1. *Average chemical compositions of major minerals in the Big Rock Donga meteorite*

oxide	weight %			
	olivine	orthopyroxene	clinopyroxene	plagioclase
SiO_2	38.5	54.8	51.4	62.7
TiO_2	-	0.2	0.4	0.1
Al_2O_3	0.1	0.2	0.4	21.1
FeO	18.7	11.3	3.0	0.3
MnO	0.5	0.6	0.2	0.1
MgO	42.6	30.8	16.5	-
CaO	0.04	0.6	22.4	2.6
Na_2O	-	-	0.3	8.3
K_2O	-	-	0.1	1.0
Cr_2O_3	-	0.2	1.2	
Total	100.5	98.7	95.9	96.2

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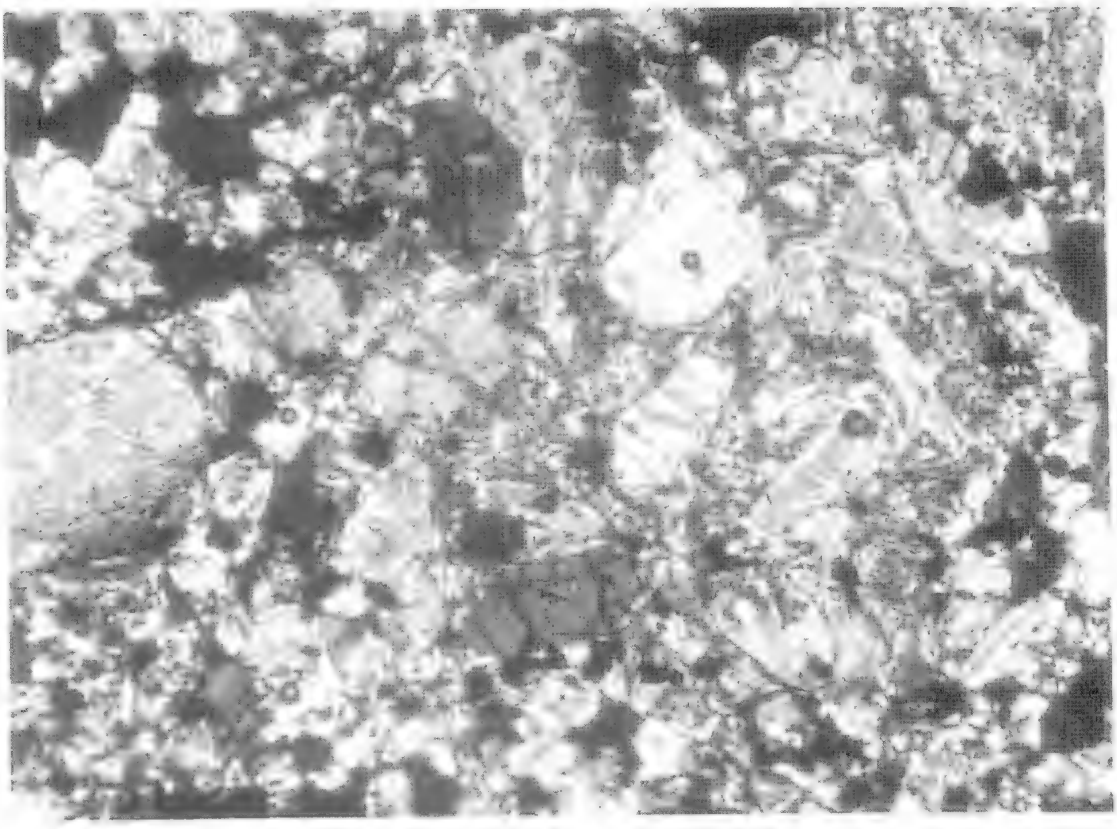

Fig. 1. Photomicrograph of the Big Rock Donga meteorite in thin section, showing a poorly defined porphyritic chondrule containing large euhedral olivine crystals in a matrix of subhedral prismatic bronzite crystals.

subhedral prismatic bronzite crystals with interstitial growths of clinopyroxene and plagioclase. Barred chondrules occur occasionally and are composed of olivine. Radial chondrules composed of orthopyroxene are also present and contain thin lamellae of either clinopyroxene or plagioclase. The matrix of the meteorite consists of slightly fractured grains of olivine and orthopyroxene (bronzite) which display very weak undulate extinction and rare grains of clinopyroxene. Plagioclase is abundant throughout the matrix as small turbid grains which also display weak undulate extinction. Nickel-iron metal, troilite, and chromite occur as accessory minerals.

Microprobe analyses show that the olivine in the Big Rock Donga meteorite is equilibrated with a mean fayalite content of $Fa_{18.8}$ (range $Fa_{18.2\text{-}19.2}$, 16 analyses). The orthopyroxene shows only a small variation in chemical composition with a mean ferrosilite content of $Fs_{16.9}$ (range $Fs_{16.5\text{-}17.8}$, 14 analyses) and a wollastonite content of 1.1 mol%. The composition of the clinopyroxene is $Wo_{46.7}En_{48}Fs_{4.9}$ (10 analyses) and that of the plagioclase is $An_{14}Or_{6.1}Ab_{79.9}$ (11 analyses).

The pyroxene geothermometers of Wells (1977) and Lindsley (1983) suggest that the Big Rock Donga meteorite was heated to temperatures of between 700° and 800°C during metamorphism while the meteorite was still part of the large H type asteroid.

Classification

Despite McCoy's initial interpretation of this meteorite as an H6 chondrite (McCoy 1991), the Big Rock Donga meteorite has been classified as an H5 chondrite. The olivine composition ($Fa_{18.8}$) is within the range of the H chondrites (Keil & Fredriksson 1964), and the orthopyroxene composition ($Fs_{16.9}$) shows that the meteorite belongs to the olivine-bronzite chondrite group. The highly equilibrated mineral compositions, crystalline matrix, poorly defined chondrule boundaries, suggest that Big Rock Donga

belongs to the type 5 classification of Van Schmus & Wood (1967). The wollastonite content in the orthopyroxene is similar to that found in other H5 chondrites (Scott *et al.* 1986). The presence of weak undulatory extinction in olivine and plagioclase grains and the degree of crystal fracture all indicate that the meteorite has been weakly shocked after metamorphism. According to the classification scheme of Stöffler *et al.* (1991), the shock facies is estimated to be S2, very weakly shocked.

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A NEW SPECIES OF *LECHRIODUS* BOULENGER (ANURA: LEPTODACTYLIDAE) FROM THE EARLY EOCENE OF QUEENSLAND

BY M. J. TYLER & H. GODTHELP†*

Summary

Lechriodus casca sp. nov. numerically is the dominant species in a collection of ilia obtained at Murgon in South-east Queensland. Radiometric dating of illites that form part of the matrix of mammalian material taken there is 54.6±0.05 million years. Accordingly *L. casca* is the earliest frog fossil known from Australia. The principal significance of the discovery of this material is the demonstration that generic differentiation at least in part antedates the separation of Australia from Antarctica, and that the dominant anuran genus of the Oligo-Miocene also was dominant in the Eocene.

KEY WORDS: *Lechriodus,* new species, ilia, Leptodactylidae, Tertiary, Queensland.

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KEY WORDS: *Lechriodus*, new species, ilia, Leptodactylidae, Tertiary, Queensland.

Introduction

The leptodactylid (myobatrachid of some authors) genus *Lechriodus* Boulenger comprises four extant species restricted to Australia and New Guinea. Amongst the 22 genera of Australopapuan leptodactylid frogs recognised, four are represented on both landmasses and are the only ones in New Guinea (*Crinia*, *Lechriodus*, *Limnodynastes* and *Mixophyes*). *Lechriodus* is unique amongst that group in having more species in New Guinea (three) than in Australia (one) (Zweifel 1972). The nature of the geographic distribution of *Lechriodus* also is unusual, for in all of the other genera common to both landmasses, representatives exist on the adjacent shorelines, whereas the solitary species in Australia (*L. fletcheri* Boulenger) is confined to the eastern seaboard of New South Wales, and its northern limit is north of the Queensland border. The northern limit in Australia is approximately 2000 km distant from the nearest congener in New Guinea (Zweifel 1972; McDonald & Miller 1982).

The fossil record partially bridges the geographic gap in the distribution of extant species because *L. intergerivus* Tyler, 1989 is known from Oligo-Miocene sites at Riversleigh Station south of the Gulf of Carpentaria, in northern Queensland.

Here we report a further new species of *Lechriodus* from an early Eocene site at Murgon, 160 km northwest of Brisbane. It represents the earliest frog fossil material yet found in Australia. The biogeographic and systematic significance of the new species is discussed elsewhere (Tyler & Godthelp in prep.).

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Material and Methods

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

Comparative studies are based on osteological collections in the Department of Zoology, University of Adelaide, with fossil material from Riversleigh being processed at the time of these studies, and with scanning electron micrographs included in Tyler (1989).

Osteological nomenclature follows Tyler (1976, 1989). Scanning electron micrographs were prepared on a Cambridge Autoscan.

Systematics

Family: Leptodactylidae Werner, 1896
Sub-family: Limnodynastinae Tyler, 1978
Genus: *Lechriodus* Boulenger, 1882

The definition of the generic characteristics of the ilium of *Lechriodus* of Tyler (1976) has been expanded by Tyler (1979). A distinguishing feature of the genus is the high dorsal crest extending for the entire length of the ilial shaft.

Lechriodus casca sp. nov
FIGS 1-3

Holotype: QM F24824, a left ilium located at Main Quarry, Boat Mountain area, Murgon (Latitude 26°15′S; Longitude 151°57′E), southeast Queensland. Tingamarra Local Fauna.

Description of holotype: The proximal portion of the ilium lacks the greater portion of the acetabular fossa, and both the dorsal and ventral acetabular expansions (Fig. 1). The shaft bears a conspicuous concave dorsal

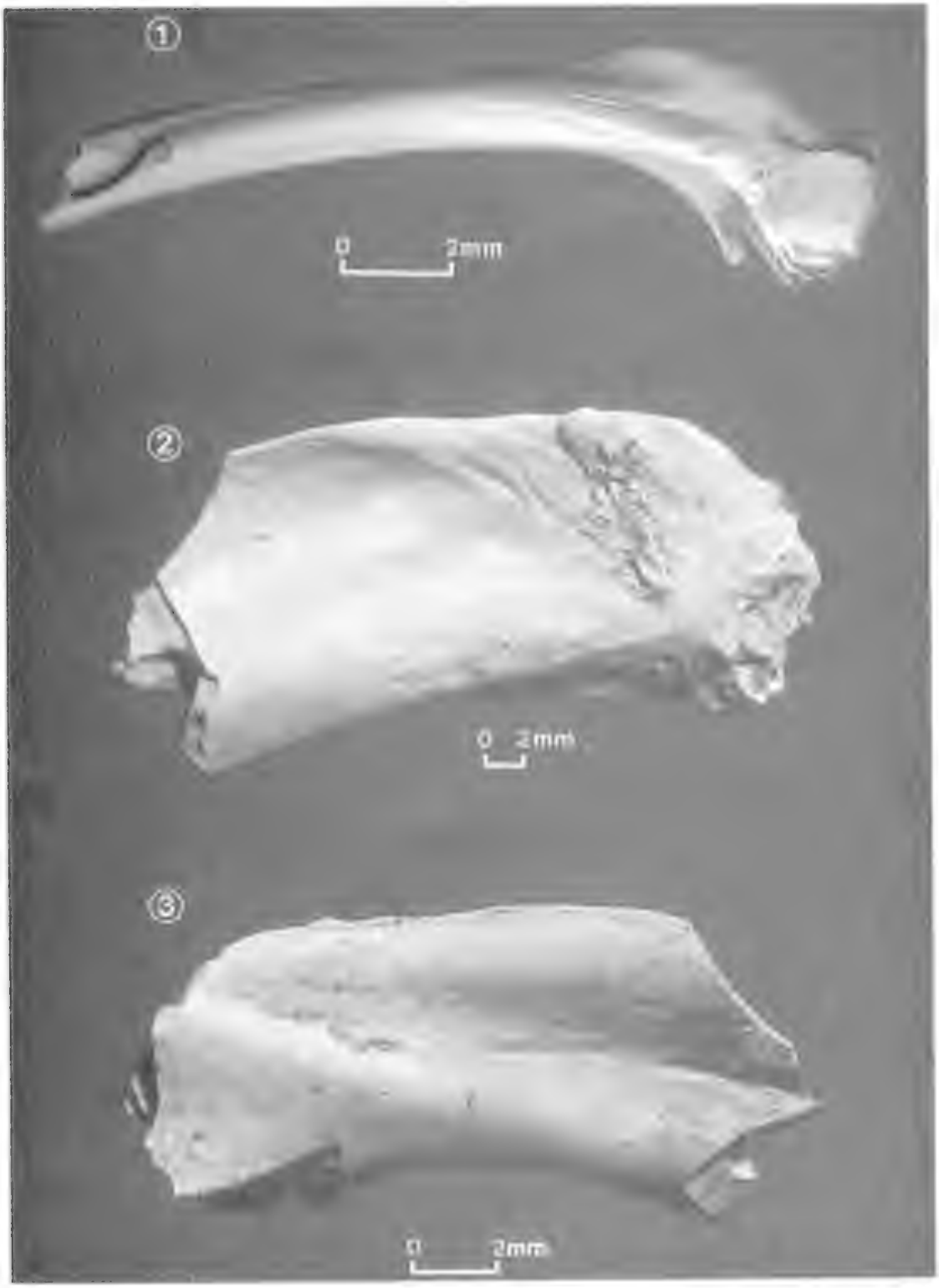

Fig. 1. (QM F24824) Holotype of *Lechriodus casca* sp. nov. 2. (QM F33558) Paratype of *Lechriodus casca* sp.nov.: lateral view. 3. medial view.

crest proximally. The medial surface bears a conspicuous, longitudinal indentation which is shallow and weakly rounded proximally and deeper and angular distally. The total length is 11.8 mm.

Paratypes: 34 ilia – QM F20197, 20216, 20243, 20565, 20567, 20689-93, 20912, 21395, 23018, 23208, 23279, 24824-28; SAM P31700, 31703-06, 31710, 33558-65. All specimens were collected at Main Quarry, Boat Mountain, Murgon.

Variation: All of the paratypes are fragmentary, but SAM P33558 (possessing a dorsal crest — Figs 2, 3) exhibits most of the features lacking in the holotype. The dorsal acetabular expansion is poorly developed whilst the pre-acetabular zone is evenly curved. The most complete shaft is that of QM F24824 which is 11.8 mm. It is unlikely that any of the type series would have a complete ilial length greater than 15 mm.

Comparison with other species: *Lechriodus intergerivus* Tyler (1989) is the only known Tertiary member of the genus and completely dominates the frog fauna at sites at Riversleigh Station during much of the Oligocene and Miocene (Tyler *et al.* 1990). From that species *L. casca* is distinguished most readily by the absence of any proximal tapering of the dorsal crest and by the very poor development of the dorsal acetabular expansion (*vide* Tyler 1989, Figs 2, 3).

Etymology: L. "casca", old.

Stratigraphy and Lithology

The anuran and mammalian fossil remains have been recovered from authigenic illite/smectite clays which are part of a sequence of clays and dolomites. Illites from this horizon have been dated radiometrically and have revealed a minimum age of 54.6±0.05 Myr. A minimum age estimate of 29.0±0.2 Myr was obtained from Potassium/Argon dating of a superpositional basalt (Godthelp *et al.* 1992).

Discussion

Lechriodus is the dominant anuran genus in the Tertiary of Queensland, constituting 28-82% of individual ilia located at sites at Riversleigh Station (Tyler *et al.* 1990) and with the lower percentages found at the more recent sites. This trend of an early dominance of *Lechriodus* has been maintained as work on the Riversleigh Station sites continues and more ilia are recovered. As at 6.xi.92, 1114 ilia had been recovered and identified and 562 (50%) represent *L. intergerivus*.

The recovery of a new species of *Lechriodus* dominating the fauna at the early Eocene site at Murgon extends the known antiquity of the genus to almost 55 million years. The biogeographic and systematic significance of the find are discussed by Tyler & Godthelp (in preparation).

Acknowledgments

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A NEW AUSTRALIAN SPECIES OF *CALODEMA* (COLEOPTERA: BUPRESTIDAE)

BY S. BARKER

Summary

A new species of *Calodema, C. rubrimarginatum* sp.nov. is described from Queensland. The species is spectacularly coloured and increases to four the number of recognised species in Australia.

KEY WORDS. Coleoptera, Buprestidae, new species, *Calodema.*

Transactions of the Royal Society of S. Aust. (1993), **117**(4): 191-192.

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by S. BARKER

Summary

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KEY WORDS: Coleoptera, Buprestidae, new species, *Calodema*.

Introduction

The genus *Calodema* LaPorte & Gory, 1837, erected to accomodate *C. regale*, comprises a number of large and spectacular species found in rainforest in Australia and New Guinea and some adjacent islands. Adults feed on flowering trees high in the canopy of the forest and are particularly difficult to collect. The species described below has been collected recently in Queensland for the first time. A revision of the genus is in preparation.

Calodema rubrimarginatum sp.nov.
FIG. 1

Holotype: ♂, Rex Ra., Qld, 3.ii.1993, J. Hasenpusch, Queensland Museum T13006.

Department of Zoology, University of Adelaide, S. Aust. 5005.

Allotype: ♀, same data as allotype, A. Hay, Queensland Museum T13007.

Colour. Head green with purple reflections. Antennae green with gold reflections. Pronotum and scutellum green with purple reflections. Elytra yellow with narrow black basal margin; triangular blue-green mark with truncated apex at spines; red margin commencing at humeral callus, thickening apically.

Shape and sculpture. Head punctuation fine, even, dense; median impressed basal line; frons moderately hairy. Pronotum normal, L:W 0.65, punctuation fine, moderately dense, stronger and denser laterally; sides rounded from base to ⅓ distance to apex, then explanate and converging anteriorly; anterior margin bisinuate, basally feebly bisinuate; median lobe truncate, median impressed line from base to ⅓ distance to anterior margin. Scutellum scutiform, anterior margin straight, concave, without punctures,

Fig. 1a. Habitus illustration and b. Lateral view of *Calodema rubrimarginatum* sp.nov. holotype. Scale bar = 1 cm.

0.16 width of elytron. Elytra slightly wider than thorax; elytral interneurs long, jointed basally, with fine, shallow, dense punctuations, scutellary striole weak; short secondary interneurs inserted between primaries 1 and 2, longer between primaries 3 and 4, 5 and 6, 7 and 8 with additional punctuations on shoulders; intervals flat, sides subparallel then tapering to pre-apical areas; apex bisinuate, both spines small, interval between sinuous and projecting close to medial spine, lateral spine anterior to medial spine. Prosternum hairy, smooth medially almost devoid of hair; hairy and finely punctuated at the sides. Conical process with well defined anterior projection in female, smaller in male; proepisternum with coarser punctuations, dense medially, very sparse almost smooth laterally, with deep smooth fossa in posterior angle. Mesosternum and metasternum smooth medially, hairy with fine moderately dense punctuation laterally. Abdomen smooth and shiny, punctuations very fine; S7: male deeply concave; female truncate.

Size: Male 34.0 × 13.5 mm (l). Female 36.3 × 14.3 mm (l).

Remarks: This species differs from the three Australian congeners in the following ways: *C. regale* and *C. wallacei*, have round colour spots on the pronotum and neither has a red margin; *C. plebeium* has an entirely red pronotum and red elytra with black fascia.

Etymology: Derived from *rubrico* L., red and *margino* L., margin.

Acknowledgments

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FIRST SOUTH AUSTRALIAN RECORD OF THE CARRION-BREEDING BLOWFLY *CALLIPHORA NIGRITHORAX* MALLOCH (DIPTERA: CALLIPHORIDAE)

BY J. F. WALLMAN

Summary

Transactions of the Royal Society of S. Aust. (1993), **117**(4), 193.

BRIEF COMMUNICATION

FIRST SOUTH AUSTRALIAN RECORD OF THE CARRION-BREEDING BLOWFLY *CALLIPHORA NIGRITHORAX* MALLOCH (DIPTERA: CALLIPHORIDAE)

Carrion-breeding blowflies are important ecologically, medically and forensically[1]. In view of the difficulties encountered in identifying them, it is therefore crucial that their distributions should be fully documented. This paper records for the first time the occurrence of one such species, *Calliphora nigrithorax* Malloch, 1927[2], in South Australia.

Recently, a single female of *C. nigrithorax* was collected in a liver-baited trap on the North Terrace campus of the University of Adelaide (20.vii.1993). *C. nigrithorax*, together with its sister species *C. ochracea* Schiner, 1868[3], is distinctive among Australian *Calliphora* in having dense erect yellow hairs on the eyes and an entirely reddish abdomen. It is distinguished from *C. ochracea* by whitish pruinescence (dusting) on the mesonotum rather than yellowish[2].

Publications defining the distributions of Australian *Calliphora* record *C. nigrithorax* as restricted to Tasmania[4,5]. These are clearly incorrect, on account of both the current record, and the holdings of the species in the Australian National Insect Collection, Canberra, in which there are specimens not only from Tasmania, but also New South Wales, the Australian Capital Territory, and Victoria[6]. The occurrence of *C. nigrithorax* in these regions was in fact first recognised in 1937[7]. Prior to my find the most westerly record of the species was from Myers Creek in Victoria (36°23'S, 144°16'E)[6]. The new record therefore extends its known range on the mainland westwards by about 500 km.

The biology and ecology of *C. nigrithorax* are poorly known. It appears to prefer cool, moist localities. The fact that I have not previously collected this species in two years of widespread trapping of blowflies in southern South Australia suggests that it may have very specialised habitat or breeding requirements. Its sister species is only locally common in the regions from which it is known, and while apparently never having been found in carcasses or live sheep in the field, has readily oviposited in thick fur in captivity[8]. *C. nigrithorax* may be similarly specialised. Alternatively, it may be a rare generalist.

Whatever the case, now that *C. nigrithorax* is known from South Australia, all workers concerned with native blowflies, in particular forensic entomologists and those studying the ecology of carrion, should henceforth consider the possibility of encountering this species in the mesic regions of the State.

I gratefully acknowledge the facilities and financial support of the Department of Zoology, University of Adelaide. I thank Dr K. R. Norris for valuable discussion and guidance, and Dr A. Wells, Dr D. A. Duckhouse and Dr A. J. Boulton for their helpful comments on the manuscript.

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ERRATA, CORRIGENDA, ADDENDA

Summary

Errata, Corrigenda, Addenda

SHIEL, R. J. & KOSTE, W. (1992) Rotifera from Australian inland waters VIII. Trichocercidae (Monogononta). *Trans. R. Soc. S. Aust.* **116**(1), 1-27.

In the **Key to species of Trichocerca known from Australia**, page 6, couplet 30 should lead to 31 and 32 respectively.

Fig. 4:2, page 7, depicts *Trichocerca bidens* (Lucks) which also is shown in Fig. 1:1, not *Trichocerca cavia* (Hudson & Gosse). The appropriate figure of *T. cavia* is as follows:

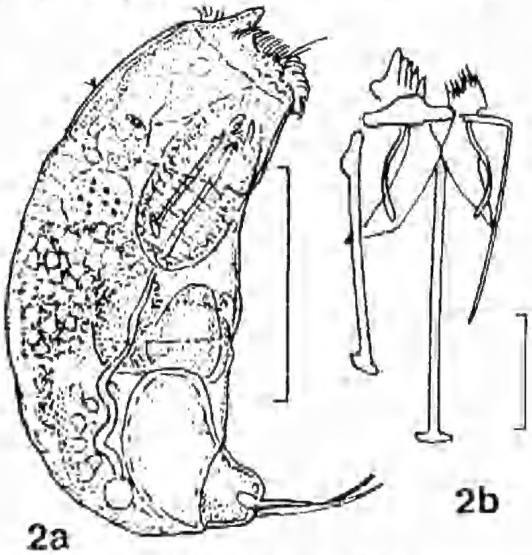

Fig. 11, p. 21: 1a, 1b should be 2a, 2b *(T. iernis)*, 2 should be 3 *(T. jenningsi)* and 3 should be 1 *(T. gracilis)*.

In the first paragraph of *Other species of Trichocerca*, page 26, we referred to other taxa of which we had only single individuals. One of these, collected by John Green, was found in a shallow roadside drain near Wodonga, Vic. It was photographed, the trophus cleared in hypochlorite and drawn, and the animal provisionally called "*T. kostei*" in recognition of Walter Koste's contribution to rotifer research in Australia. The material was put aside until more specimens could be found.

Subsequently, a manuscript on Nigerian rotifers was received for comment (by RJS) in Sept. 1992, in which a new trichocercid was described. Despite minor differences in trophus structure, it was apparently the same species as the specimen from the Barnawartha-Wodonga Rd pool, and by remarkable coincidence, it was named *T. kostei*! It can now be added to the known *Trichocerca* species from Australia.

Trichocerca kostei Segers

Trichocerca kostei Segers, 1993, p. 59-60, Fig. 24.

Type locality: Oguta Lake littoral, Imo State, Nigeria.
Holotype: Female No. 821, Royal Museum for Central Africa (MRAC), Tervuren, Belgium.
Paratypes: Two females (MRAC 822) and one female and one trophus preparation in the collection of the State University of Ghent, Belgium.
Description: Body elongate, slightly curved, with dorsal keel to ca. half body length (Fig. 1 a); broad lateral triangular projection on right side of head (dorsal), with ventral emargination; foot short; left toe 2X right, both curved; three substyli per toe; trophus (Fig. 1b, cf. the Victorian specimen, c.) resembles that of *T. porcellus, T. tigris, T. uncinata*: strongly asymmetric, with reduced right manubrium and uncus; right ramus with distinctive finger-like alula parallel to fulcrum; left manubrium large, terminally widened into boomerang shape; unci teeth fused, massive; fulcrum long, terminates in distal disc.

BL 178-196 μm; BW 46-54 μm; LT to 108 μm; RT to 54 μm; TR 65-70 μm.

Distribution: Only two locations known to date, the type locality in Nigeria and a flowing (?ephemeral) roadside pool, 10 km south of Wodonga on Wodonga-Barnawartha Rd, north-eastern Victoria (MDFRC Site #3194, 09.IX.91, Coll. J.D. Green). Vegetated littoral, 14.5 °C, pH 8.8, 153 μS cm^{-1}.

Comment: The single Victorian specimen has a longer left manubrium (42 μm vs 40 μm). This difference is accentuated in the different perspectives drawn below. The apparent difference in the distal manubrium of the local specimen (Fig. 1c below), which is more spatulate than that of the type, may also be a perspective artefact.

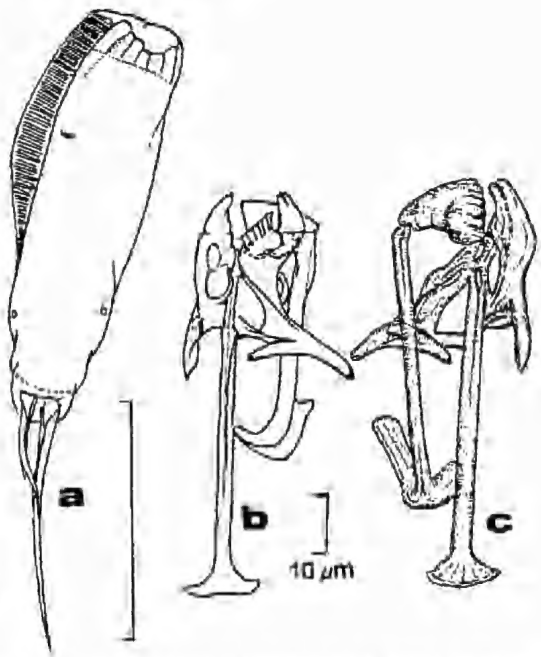

Fig. 1: *Trichocera kostei* a, ventral view; b, trophus, ventral, Nigerian specimen; c, trophus, dorsal, Victorian specimen. a, b after Segers (1993).

Acknowledgment

For permission to use figures of *T. kostei* from Segers (1993), thanks to Henri Dumont, Editor, *Hydrobiologia*.

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